LIBRARY
FISH & WILDLIFE SERVICE
PACIFIC OCEANIC FISHERY
INVESTIGATIONS

WOODS HOLE OCEANOGRAPHIC INSTITUTION

COLLECTED REPRINTS

1939

MARCH, 1940

WOODS HOLE OCEANOGRAPHIC INSTITUTION

COLLECTED REPRINTS

1939

1702

LIBRARY
FISH & WILDLIFE SERVICE
PACIFIC OCEANIC FISHERY
INVESTIGATIONS

MARCH, 1940

The present volume contains the contributions from the Woods Hole Oceanographic Institution which appeared during 1939 in publications other than *Papers in Physical Oceanography and Meteorology;* also the Annual Report of the Director for 1938.

TABLE OF CONTENTS

Contribution
No.

173. FLOYD M. SOULE
Oceanography. Excerpt from International Ice Observation and Ice Patrol Service in the North Atlantic, Season of 1937. Published in 1938

191. JEAN P. TODD
Shoal-water Deposits of the Bermuda Banks

192. H. R. SEIWELL
Die Verwendung der Verteilung von Sauerstoff auf die physische Ozeanographie des Karibischen Meeresgebietes

193. GEORGE L. CLARKE and HARRY R. JAMES
Laboratory Analysis of the Selective Absorption of Light by Sea Water

194. HENRY B. BIGELOW and MARY SEARS
Studies of the Waters of the Continental Shelf, Cape Cod to Chesapeake Bay. III. A Volumetric Study of the Zooplankton

195. GEORGE WALD
On the Distribution of Vitamins A_1 and A_2

196. ALFRED C. REDFIELD
The History of a Population of *Limacina retroversa* during its Drift across the Gulf of Maine

197. SIDNEY C. T. HSIAO
The Reproductive System and Spermatogenesis of *Limacina (Spiratella) retroversa* (Flem.)

199. FENNER A. CHACE, JR.
Reports on the Scientific Results of the first *Atlantis* Expedition to the West Indies, under the joint auspices of the University of Havana and Harvard University. Preliminary descriptions of one New Genus and Seventeen New Species of Decapod and Stomatopod Crustacea

201. GEORGE L. CLARKE
The Utilization of Solar Energy by Aquatic Organisms

202. CLINTON M. OSBORN
The Physiology of Color Change in Flatfishes

203. MARTIN D. BURKENROAD
Further Observations on Penaeidae of the Northern Gulf of Mexico

204. FRED B. PHLEGER, JR.
Foraminifera of Submarine Cores from the Continental Slope

205. TALBOT H. WATERMAN, RUDOLF F. NUNNEMACHER, FENNER A. CHACE, JR., and GEORGE L. CLARKE
Diurnal Vertical Migrations of Deep-water Plankton

206. SIDNEY C. T. HSIAO
The Reproduction of *Limacina retroversa* (Flem.)

Contribution
No.

207. W. H. JOHNSON and J. E. G. RAYMONT
The Reactions of the Planktonic Copepod, *Centropages typicus*, to Light and Gravity

208. LOUIS A. TOTH
Renal and Vascular Responses to Epinephrine Injections in Glomerular and Aglomerular Fish

209. JOHN A. YOUNG, JR.
Minerals from Deep Sea Cores and Surface Deposits of Bermudian Calcareous Sediments

210. HENRY B. BIGELOW and WILLIAM C. SCHROEDER
Notes on the Fauna above Mud Bottoms in Deep Water in the Gulf of Maine

211. TALBOT HOWE WATERMAN
Studies of Deep-sea Angler-fishes (Ceratioidea)

212. GEORGE L. CLARKE
The Relation between Diatoms and Copepods as a Factor in the Productivity of the Sea

213. A. A. ABRAMOWITZ
The Pituitary Control of Chromatophores in the Dogfish

214. GEORGE L. CLARKE and DAVID D. BONNET
The Influence of Temperature on the Survival, Growth and Respiration of *Calanus finmarchicus*

216. BOSTWICK H. KETCHUM
The Absorption of Phosphate and Nitrate by Illuminated Cultures of *Nitzschia Closterium*

217. H. R. SEIWELL
Some Applications of Statistical Methods to Problems in Modern Physical Oceanography

218. PEDRO J. BERMÚDEZ
Resultados de la Primera Expedicion en las Antillas del Ketch *Atlantis* bajo los Auspicios de las Universidades de Harvard y Habana. Nueva Género y Especies Nuevas de Foraminiferos

219. BOSTWICK H. KETCHUM
The Development and Restoration of Deficiencies in the Phosphorus and Nitrogen Composition of Unicellular Plants

220. C. O'D. ISELIN
The Influence of Vertical and Lateral Turbulence on the Characteristics of the Waters at Mid-depths

221. C. O'D. ISELIN
Some Physical Factors which may Influence the Productivity of New England's Coastal Waters

Contribution
No.

222. THEODOR VON BRAND, NORRIS W. RAKESTRAW and CHARLES E. RENN
Further Experiments on the Decomposition and Regeneration of Nitrogenous Organic Matter in Sea Water

223. H. R. SEIWELL
Atlantis Cruise to the Tropical North Atlantic, January to March, 1939

224. W. J. CLENCH and C. G. AGUAYO
Notes and Descriptions of New Deep-water Mollusca obtained by the Harvard-Havana Expedition off the Coast of Cuba. II

225. PEDRO J. BERMÚDEZ
Resultados de la Primera Expedicion en las Antillas del Ketch *Atlantis* bajo los Auspicios de las Universidades de Harvard y Habana. Foraminiferos del Género Recurvoides, descripción de una Especie Nueva

227. H. R. SEIWELL
Daily Temperature Variations in the Western North Atlantic

228. NORRIS W. RAKESTRAW, CLIFFORD E. HERRICK, JR., and WM. D. URRY
The Helium-Neon Content of Sea Water and its Relation to the Oxygen Content

229. EDWARD M. BROOKS
Transport and Convergence of the North Atlantic Drift Current computed from the Average January Pressure Distribution

230. FLOYD M. SOULE
Consideration of the Depth of the Motionless Surface near the Grand Banks of Newfoundland

232. GORDON A. RILEY
Plankton Studies. II. The Western North Atlantic, May-June, 1939

233. J. T. NICHOLS
Young Caranx in the Western North Atlantic

234. ALBERT EIDE PARR
Quantitative Observations on the Pelagic Sargassum Vegetation of the Western North Atlantic

236. GEORGE L. CLARKE
Variation in the Transparency of Three Areas of the Atlantic throughout the Year

238. D. Q. ANDERSON
Distribution of Organic Matter in Marine Sediments and its Availability to Further Decomposition

243. PEDRO J. BERMÚDEZ
Resultados de la Primera Expedicion en las Antillas del Ketch *Atlantis* bajo los Auspicios de las Universidades de Harvard y Habana. Nueva Género y Especies Nuevas de Foraminiferos

THE WOODS HOLE OCEANOGRAPHIC INSTITUTION
Report for the year 1938

LIST OF CONTRIBUTIONS

Contribution No. 173

UNITED STATES TREASURY DEPARTMENT

COAST GUARD

Oceanography

Season of 1937

Reprint From Bulletin No. 27, International Ice Observation and
Ice Patrol Service in the North Atlantic Ocean

* * *

UNITED STATES GOVERNMENT PRINTING OFFICE
WASHINGTON: 1938

OCEANOGRAPHY [1]

By Floyd M. Soule

The *General Greene* departed from Woods Hole on March 24, 1937, stopping at Halifax with parts for the *Mendota* enroute to the Grand Banks, where the work of making a current survey began on March 31 at station 2265 located at 43°54′ N., 53°54′ W. In view of the reported location and drift of early-season ice southward from the Avalon Peninsula of Newfoundland, it was deemed advisable to include in this survey the southwestern slope of the Grand Banks. Work progressed without major incident until the completion of station 2290 in 41°40′ N., 49°20′ W., on April 4, when conditions of wind and sea caused the omission of two proposed stations located southeastward of this position. Station work was resumed at station 2291 in 41°56′ N., 46°59′ W., on April 6 and continued until April 10, when the collection of data was completed at station 2315 in 44°28′ N., 46°55′ W., a total of 51 stations having been occupied. Two additional sections northward of latitude 45° had been planned but had to be eliminated in order to retain a fuel reserve sufficient to reach Halifax in the event that the harbor of St. John's, Newfoundland, could not be entered because of the field ice which had been prevalent along the Avalon Peninsula during the spring. The resulting current chart was then constructed and delivered to the *Mendota* 20 hours after the last station had been completed. The *General Greene* then proceeded toward Cape Race, skirting the coast inside the ice to St. John's, where she arrived on April 13.

On April 26 the *General Greene* departed from St. John's for the purpose of making a second current map of the region in the vicinity of the Grand Banks believed to be critical with respect to the drift of menacing ice. In order to insure getting data from that part of the area immediately southward of latitude 47° N., and to take advantage of a waning moon it was decided to work from the north towards south.

Accordingly, the work of collection of data began at station 2316, located at 46°58′ N., 48°41′ W., on April 27. Aside from occasional delays arising from mechanical difficulties, the work progressed without interruption. Collection of data was completed at station 2389 at 42°00′ N., 52°00′ W., on May 9, a total of 74 stations having been occupied. The resulting current map was then constructed and although it was finished 9 hours after the last station had been completed, delivery could not be effected until the *Mendota* could be contacted the next morning, May 10. After the map was delivered aboard the patrol cutter, the *General Greene* proceeded to St. John's where she arrived on May 11.

---

[1] Contribution No. 173 of the Woods Hole Oceanographic Institution.

The *General Greene* departed from St. John's on May 25 to make a third current survey. The reported distribution of what few bergs seemed destined to travel the eastern branch of the Labrador Current indicated that current information was desirable from the area east of the Grand Banks and immediately northward of latitude 47° N., in addition to information from the usually surveyed area to the southward. Therefore, the work of collection of data was begun at station 2390, located near the northwestern edge of Flemish Cap, on May 26. Work progressed without major interruption and was completed at station 2465 at 43°25′ N., 50°09′ W., on June 6, after 76 stations had been occupied. The resulting current map was then constructed and was delivered aboard the *Mendota* 18½ hours after completion of the last station. The *General Greene* then proceeded to St. John's arriving there on June 8.

Thus 201 oceanographic stations were occupied during the ice-patrol season. Between June 21 and July 12 an additional 75 stations were occupied on a post-season cruise which involved six sections approximately normal to the Labrador and Atlantic Currents and designed to cross their common boundary at intervals from the Tail of the Grand Banks to northeast of Flemish Cap. The temperature and salinity data collected at the 276 oceanographic stations occupied during the season and on the post-season cruise are presented in the oceanographic table in this bulletin.

On the post-season cruise, 843 sonic soundings were made with the fathometer. These have been corrected for sounding velocity by means of the concurrently collected temperature and salinity data in accordance with the temperature-salinity-pressure-velocity relations given in the British Admiralty tables (H. D. 282). The corrected soundings have been tabulated and forwarded to the United States Hydrographic Office and to the International Hydrographic Bureau.

During the ice season, and in continuation of cooperation with the Fisheries Research Laboratory of the Newfoundland Department of Natural Resources, abstracts of temperatures and salinities measured were forwarded to that laboratory promptly upon the return of the *General Greene* to St. John's at the conclusion of each survey. Other incidental data collected on the *General Greene* consisted of barograms and sea-water surface thermograms.

The equipment and methods of measurements were the same as in 1936. Routine salinity bridge measurements and calibration titrations were performed by the oceanographer's assistants, Bernard S. Leobig, yeoman, first-class, and James F. Flannery, seaman, first-class.

At the 201 stations occupied during the season, the extent and nominal depths of the serial observations of temperature and salinity where the same as during the season of 1936. On the post-season cruise the observations were carried to as near bottom as was practical at most of the stations in the region southwestward of Flemish Cap and to 2,000 meters at the remaining stations.

As a check on the functioning of the reversing thermometers, a program of intercomparison through periodic shifts in thermometer pairs was carried out as in 1936. A total of 1,378 individual comparisons were investigated. The probable differences between the corrected readings of a pair of thermometers varied among the different groups from 0.002° to 0.015° C. and the probable difference for the entire 1,378 comparisons was 0.007° C. It is therefore considered that the observed temperatures are accurate to 0.01° C.

The current maps prepared during the season were made following the procedure used in 1936, the season's maps being referred to the 1,000-decibar surface. The current map representing conditions found on the post-season cruise is referred to the 2,000-decibar surface.

In figure 34 is shown the current map resulting from the first survey, March 31 to April 10. This map shows a small part of the Labrador Current rounding the Tail of the Grand Banks to the westward before curving south and east. A small pool of cold water is shown southwestward of the Banks and a larger pool southeastward of the Banks. This latter has an eastward extension which will be remarked upon later on. The maximum velocity of the Labrador Current is about normal, but the location, both of this maximum and of the westward intrusion of Atlantic Current water, is some 40 miles south of the usual location. The Grand Banks whorl was comparatively inactive, but, as the whorl is believed to be partly energized by the vernal warming over the southeastern shoal, its inactivity is in accord with the early date of the observations. The edge of the Atlantic Current is to be seen at the eastern border of the map.

Figure 35 shows the current map made from data collected on the second survey, April 27 to May 9. A notable feature of this map is the amount of current coming off the Grand Banks northward of latitude 44° N. A part of this is the Grand Banks whorl but it is believed that considerable additions to the whorl from the western branch of the Labrador Current are present in this survey. That the western branch of the Labrador Current was flowing with abnormal strength is indicated by the unusual concentration of ice drifting south along the Avalon Peninsula. This western branch spreads fan-like with rapidly diminishing velocities after reaching Cape Race.

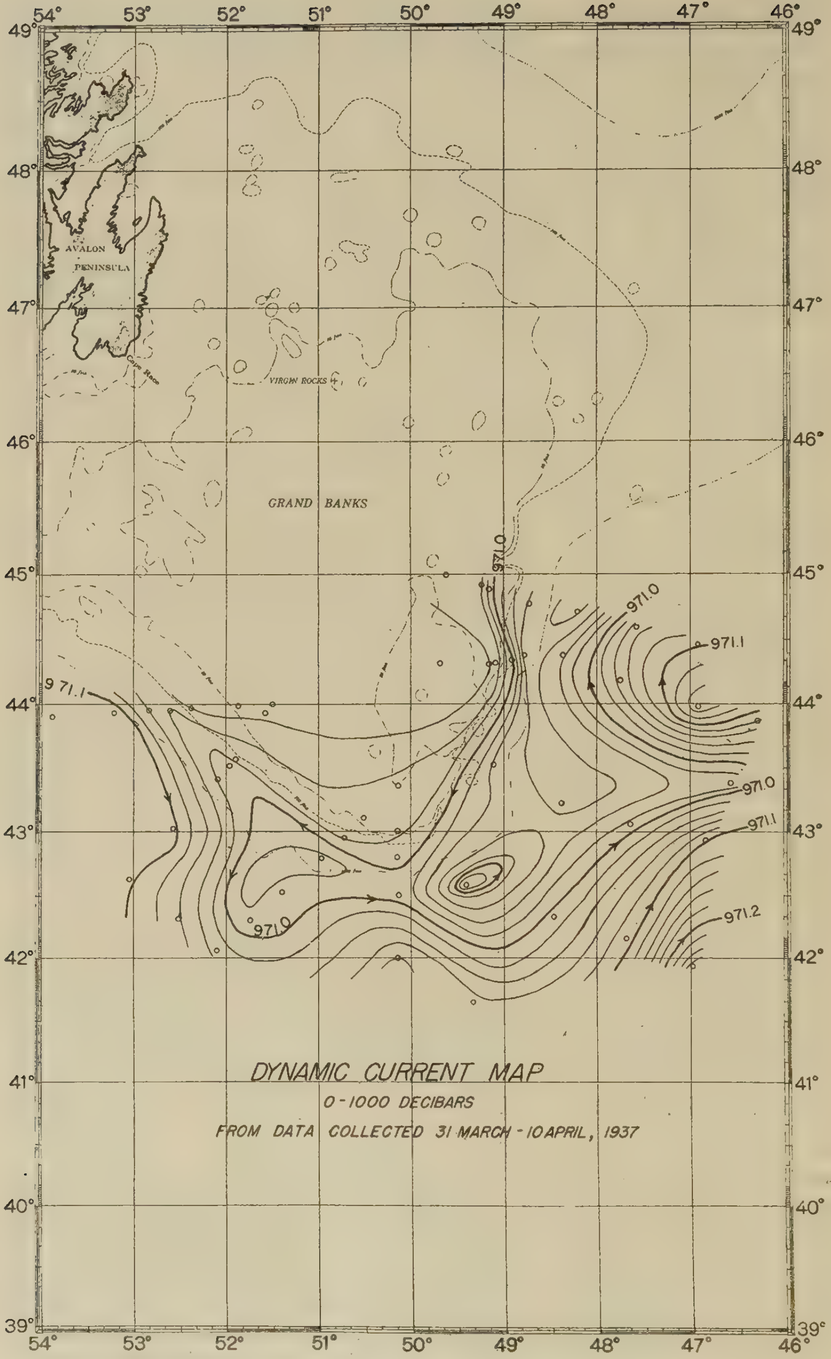

54°
53°
52°
51°
50°
49°
48°
47°
46°
39°
40°
41°
42°
43°
44°
45°
46°
47°
48°
49°
AVALON PENINSULA
Cape Race
VIRGIN ROCKS
GRAND BANKS
971.0
971.1
971.0
971.1
971.0
971.1
971.2
971.0
DYNAMIC CURRENT MAP
0-1000 DECIBARS
FROM DATA COLLECTED 31 MARCH - 10 APRIL, 1937

FIGURE 34.—Dynamic current map, from data collected March 31–April 10, 1937.

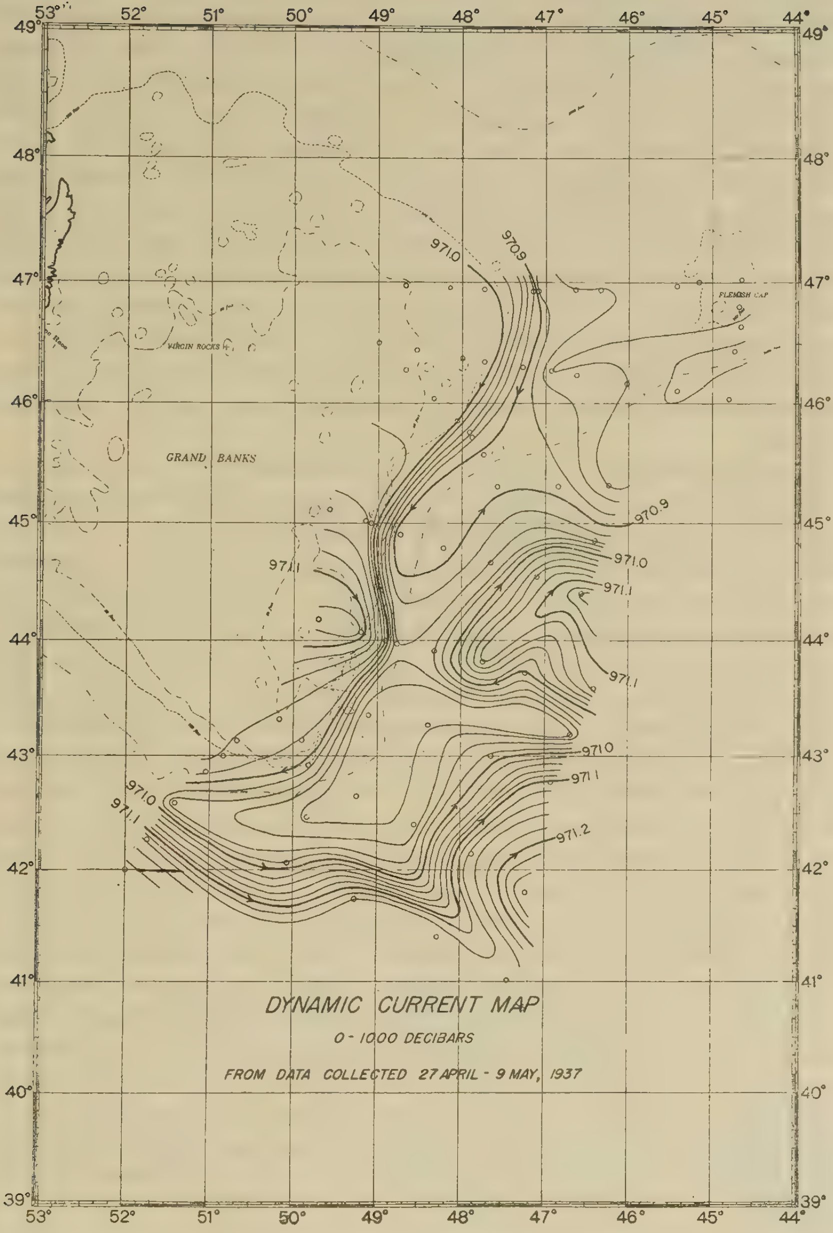

53°
52°
51°
50°
49°
48°
47°
46°
45°
44°
43°
42°
41°
40°
39°
FLEMISH CAP
VIRGIN ROCKS
GRAND BANKS
971.0
970.9
971.1
971.2
DYNAMIC CURRENT MAP
0 - 1000 DECIBARS
FROM DATA COLLECTED 27 APRIL - 9 MAY, 1937

FIGURE 35.—Dynamic current map, from data collected April 27–May 9, 1937.

The off-shore part of the western branch moves eastward across the Banks to join the eastern branch on the left and the Grand Banks whorl on the right. It is to this portion of the western branch of the Labrador Current that a considerable part of the movement of water off the Banks is attributed. The southward displacement of such characteristic features as the position of maximum velocity of the Labrador Current, the westward intrusion of Atlantic Current water, and the vortical center usually associated with Flemish Cap, was present again in this survey although not as pronounced as in the first survey. The two cold-water pools found in the first survey became larger and merged into one whose eastward extension was again noteworthy. The westward intrusion of Atlantic Current water between about 43°30′ N., and 45°00′ N., strengthened somewhat and, combined with the augmented Grand Banks whorl, succeeded in turning back to the northeastward more of the Labrador Current.

The current situation found in the third survey, May 26 to June 6, is shown in figure 36. The dynamic isobaths of this survey follow in unusual detail the features of the bottom topography. This is probably attributable to the long-continued period of quiet weather preceding the observations. Gales of short duration apparently do not permanently alter the currents. At least it has been observed that after a few days of gales the berg-drifts are still in accord with a current map made prior to the gales. However, it is also evident from a consideration of the meteorological conditions on the Labrador coast in connection with the transportation of icebergs and volume of flow of the Labrador Current, that average conditions over a period as long as a month are effective in introducing wind-current components. Consequently, it is reasonable that the above-mentioned long-continued period of quiet weather meant the absence of disturbing wind-current components and permitted the currents to follow with unusual fidelity the bottom features. The contribution of water off the Grand Banks was less vigorous than in the second survey but covered a much wider front, the center of the Grand Banks whorl having shifted southward some 60 or 70 miles. As in the first two surveys, the intrusion of Atlantic water retained its unusually southern position. The cold-water pool shown in the first two surveys was still present as indicated by the southeasternmost stations, but the survey did not extend far enough to the south to fully develop its extent.

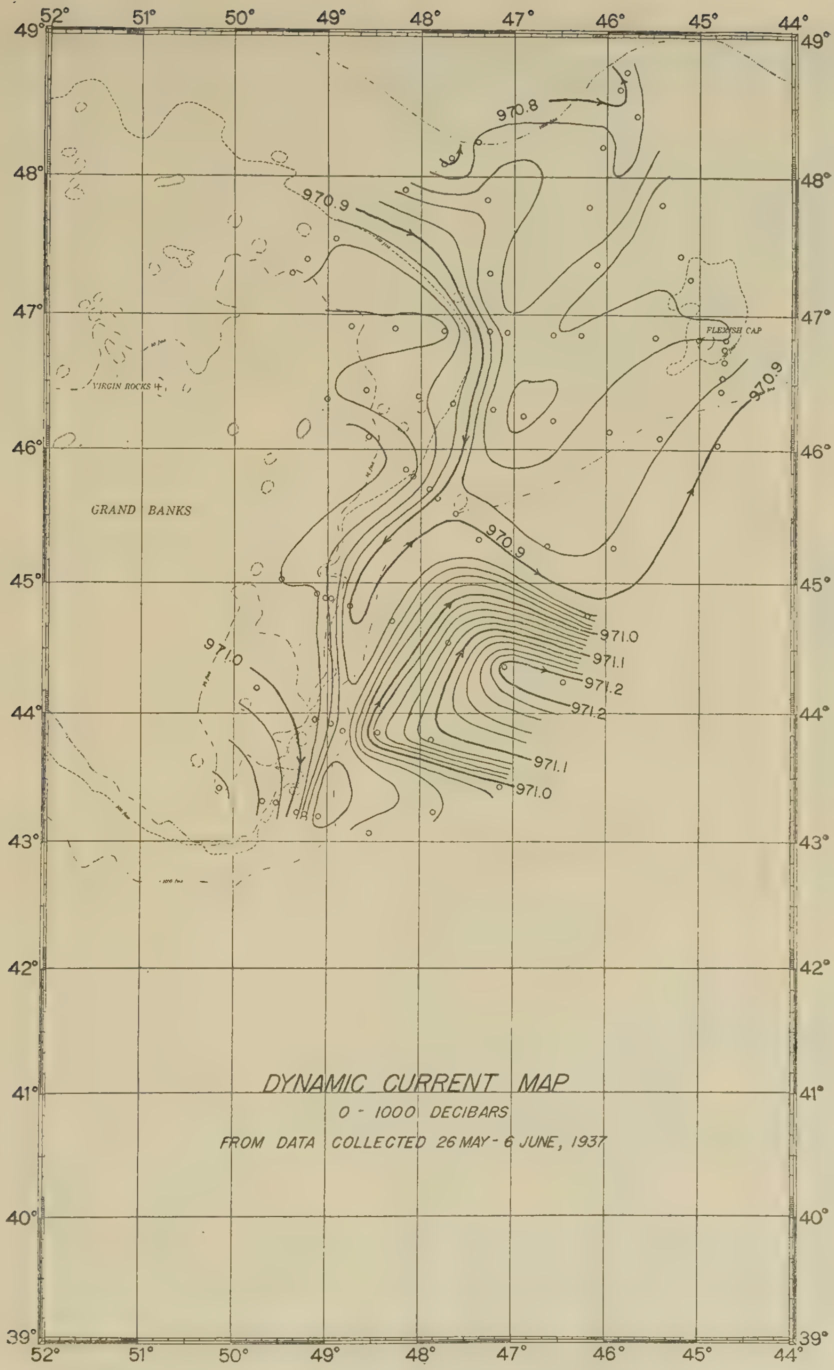

52°
51°
50°
49°
48°
47°
46°
45°
44°
43°
42°
41°
40°
39°
970.8
970.9
971.0
971.1
971.2
FLEMISH CAP
VIRGIN ROCKS
GRAND BANKS
DYNAMIC CURRENT MAP
0 - 1000 DECIBARS
FROM DATA COLLECTED 26 MAY - 6 JUNE, 1937

FIGURE 36.—Dynamic current map, from data collected May 26–June 6, 1937.

TABLE 1.—*Showing volume of flow in million cubic meters per second, mean temperature in °C, and minimum temperature in °C, of the Labrador Current in the Grand Banks region*

	Section T					Section U					Section W				
	1934	1935	1936	1937	Average	1934	1935	1936	1937	Average	1934	1935	1936	1937	Average
April:															
Volume	1.8	2.1	1.86		1.92	3.48	3.7	7.20	3.54	4.48	1.17	1.08	3.13	0.54	1.48
Mean temperature	1.53	1.67	.98		1.39	1.11	2.0	2.31	1.54	1.74	1.19	2.72	2.61	.66	1.80
Minimum temperature	−1.66	−1.71	−.75		−1.37	−1.37	−1.66	−.82	−1.29	−1.28	−1.15	−1.12	.02	−.29	−.64
May:															
Volume	1.5	4.1	3.23	3.53	3.09	3.11	5.92	6.69	5.80	5.38	1.63	3.87	8.78	5.48	4.94
Mean temperature	2.6	2.85	1.83	1.83	2.28	1.56	.98	1.06	1.90	1.38	1.07	1.47	2.85	2.33	1.93
Minimum temperature	−1.72	−1.56	−.43	−1.49	−1.30	−1.70	−1.24	−.94	−1.56	−1.35	−1.58	−1.02	.08	−.99	−.88
June:															
Volume	1.5	2.71	3.15	1.96	2.33	.84	4.46	3.90	2.29	2.87	.86				
Mean temperature	3.3	2.06	2.90	1.55	2.45	1.32	1.75	3.14	1.72	1.98	4.35				
Minimum temperature	−1.70	−1.50	−1.47	−1.22	−1.47	−1.65	−1.28	−1.23	−1.29	−1.36	1.68				
Post season:															
Volume				1.88					3.02					3.40	
Mean temperature				2.19					1.81					2.53	
Minimum temperature				−1.25					−1.41					−.76	

In United States Coast Guard Bulletin No. 26 the seasonal variation in the Labrador Current in the Grand Banks sector was discussed and evidence presented tending to show that there was a seasonal maximum volume of flow occurring during the month of May. Measurements made during 1937 confirmed this. The sections involved are as follows: Section T, running southeasterly from about latitude 46°20′ N., longitude 49°00′ W.; section U, running east and west at about 45° N.; and section W, running south off the Grand Banks in about 50° W. Section T was reoccupied May 1, June 1–2, and June 30; section U was reoccupied April 10, May 3, June 4, and June 29; and section W was reoccupied April 3–4, May 7–8, and June 21–22. The volume of flow, mean temperature, and minimum observed temperature was investigated for each occupation of these sections and the results are tabulated below along with similar results for all occupations of these sections during 1934, 1935, and 1936.

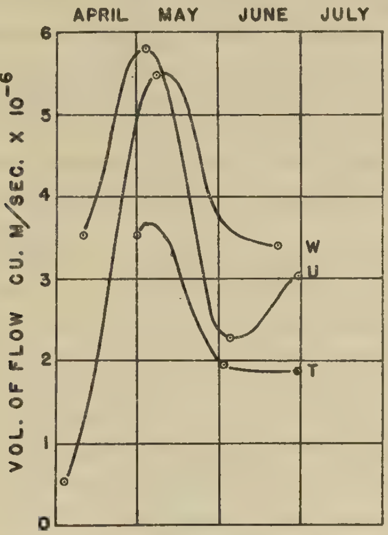


FIGURE 37.—Variation in the volume of flow of the Labrador Current in the Grand Banks region durin the 1937 season.

In figure 37 is shown graphically the seasonal variation in the volume of flow of the Labrador Current past sections T, U, and W during the 1937 season.

There is some evidence that the unusual activity of the West Greenland Current rounding Cape Farewell in 1935 was still making its effect on the Labrador Current felt. The immediate effect of this 1935 flood seems to have been the sweeping of the American side clean of bergs with the result that a greater than expected number of bergs arrived in the Banks region that year. The next effect was the warming of the offshore part of the Labrador Current through the increase in the West Greenland Current component, with a more rapid deterioration of bergs along the Labrador coast resulting in slightly fewer bergs than were expected actually appearing in the Banks region in 1936. The next and probably final effect of this flood was that in 1937 the Baffin Land component of the Labrador Current was strengthened and a greater than usual proportion of the Labrador Current followed the western branch along the Avalon Peninsula of Newfoundland and resulted in concentrating the 1937 berg crop along that branch rather than along the usual path down the eastern edge of the Grand Banks. That the cause of this spurt in the Baffin Land component of the Labrador Current was the 1935 flood of West Greenland Current seems entirely reasonable. In United States Coast Guard Bulletin No. 26 it was remarked that the effect of the flood would be dual—the freeing, along the Greenland side, of large numbers of bergs which would appear in the Grand Banks region in 1937, and the more rapid disintegration of the bergs because of the higher temperatures during the interval of travel. The disintegration effect seems to have preponderated as the number appearing was less than expected on the basis of purely meteorological considerations.

A quantitative investigation of the contribution of water eastward off the Grand Banks was attempted in order to see if any appreciable effect of the flood discussed above was evident. Jakhelln's method [2] of determining the net volume of flow between two stations was applied, taking the volume of flow to be proportional to the difference between the second depth integrals of anomaly of specific volume at the stations concerned. The stations were referred to the 1,500 decibar surface by means of Helland-Hansen's and Nansen's method. The volume of flow was thus determined for each of 12 surveys made over the 4-year period 1934–37. For each survey the northern station selected was the shallow-end terminal of section T and the southern station selected was the highest Grand Banks station of the survey indicating the center of the Grand Banks whorl. The resulting volumes of flow seem to be much too large and indicate erroneous assumptions either as to the distribution of anomaly of specific volume on bottom along the section of approach, or as to the static condition of the reference surface, or both. Nevertheless, it is believed that the errors involved are sufficiently similar to make the results useful as trend indicators, and in the absence of any other data on the subject the computed volumes of flow are shown here graphically in figure 38.

It will be noted that in 1934, 1935, and 1936 the trend is one of diminishing volume through May and June, whereas in 1937 the volume of flow maintained a high value and increased somewhat during these months. This sustained large volume of flow is looked upon as being the result of the abnormally large amount of water flowing in the western branch of the Labrador Current and traceable to the increased activity of the Baffin Land Current arising from the 1935 flood of West Greenland Current around Cape Farewell. It may or may not be significant that in 1935 the contribution of water off the Grand Banks was lower than in any of the other years investigated. The average computed volumes of flow of this contribution for the four seasons were: 1934, 3.5; 1935, 1. 4; 1936, 3. 3; and 1937, 4.5 million cubic meters per second. As previously mentioned, these magnitudes must not be accepted without reservations because they

---

[2] Jakhelln, A: The Water Transport of Gradient Currents. Geofysiske Publikasjoner. Vol. XI, No. 11; Oslo, 1936.

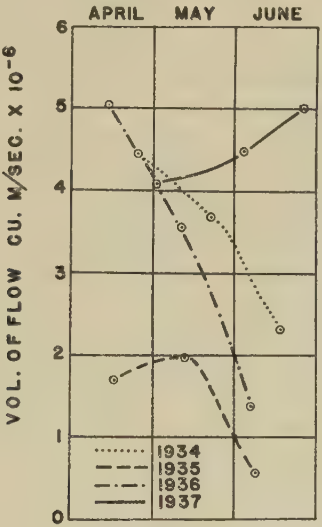


FIGURE 38.—Variation in the volume of flow of water eastward off the Grand Banks during the 4-year period 1934–37.

would require the unbelievably high average easterly velocity of about one-half nautical mile per hour.

In continuation of inquiry into the departures from average conditions along the common boundary between the Labrador and Atlantic Currents, the course of the horizontal projection of the zero salinity anomaly line in the axis of the intermediate anomaly maximum has been determined for each of the three surveys made during the 1937 season. The boundaries so indicated are shown in figure 39 along with the average course of the boundary for the four-year period 1934–37. An inspection of figure 39 indicates that during the first survey Labrador Current water covered a larger area than usual, whereas during the two following surveys the boundaries were deeply indented but the areas covered by the two types of water were close

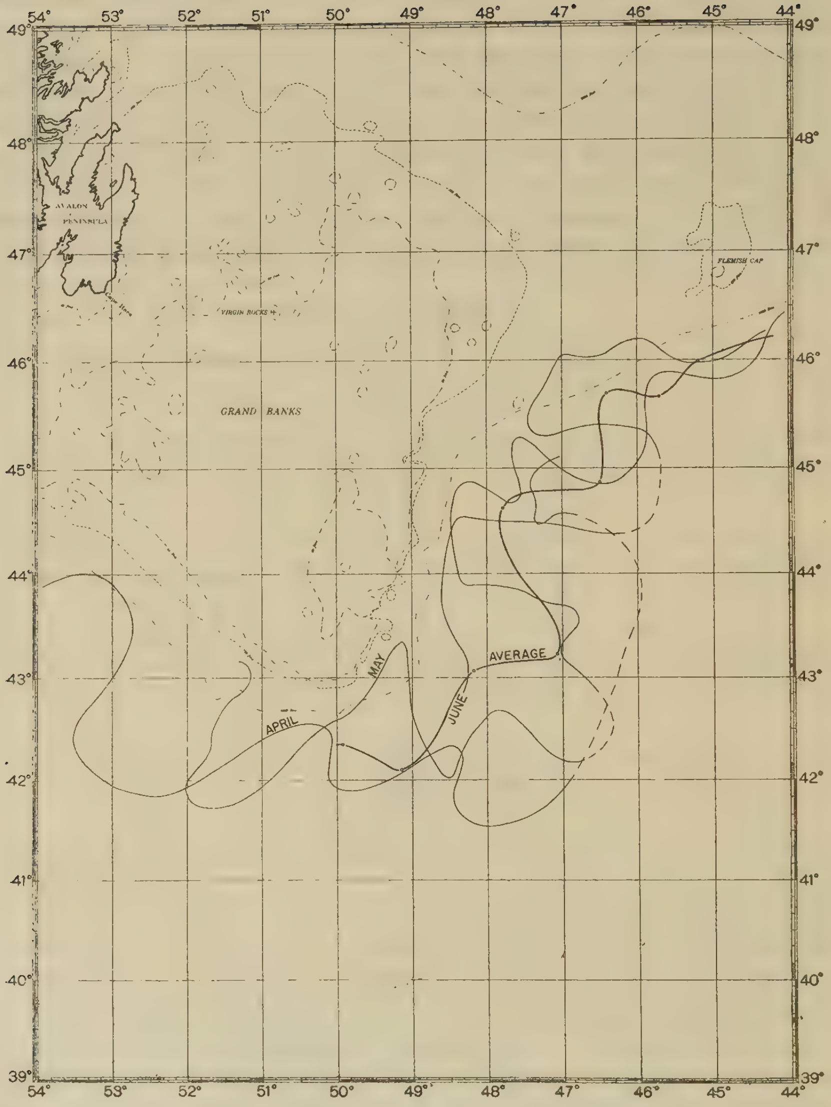

54°
53°
52°
51°
50°
49°
48°
47°
46°
45°
44°
49°
48°
47°
46°
45°
44°
43°
42°
41°
40°
39°
AVALON PENINSULA
Cape Race
VIRGIN ROCKS
FLEMISH CAP
GRAND BANKS
MAY
AVERAGE
JUNE
APRIL

FIGURE 39.—Boundary between Labrador Current water and Atlantic Current water as indicated by zero salinity anomaly at intermediate salinity anomaly maximum. 1937 season and average 1934–1937.

to the 4-year average. Such a boundary line could not be drawn satisfactorily for the post-season cruise as it was evidently outside of the area surveyed except for a few stations at about latitude 44° N., near the eastern edge of the survey. This may be looked upon as indicating either an error in standardization of salinities, or a breakdown of the criterion of the boundary, or the presence of an abnormal quantity of mixed water which derived its negative anomaly from the Labrador Current. That the last possibility is probable is supported by other evidence discussed in connection with the post-season cruise results.

POST SEASON CRUISE, 1937

As was mentioned previously in this report a post-season cruise was made in the boundary region between the Labrador and Atlantic Currents and was laid out with a view toward the occupation of several sections which would cross the major portion of these streams and their common boundary. It was also anticipated that, at least in a portion of the area, the sections would be spaced sufficiently close together so that a current map showing the main features of circulation might be derived from the results of the survey.

Prior to the construction of any maps the data were studied for the selection of a reference surface. The horizontal distribution of anomaly of specific volume was examined by means of the construction of horizontal sections for several of the deeper levels. Inspection of these sections indicated that the smallest horizontal gradients of anomaly of specific volume, and therefore probably the most nearly motionless level, occurred at 2,000 or 2,500 meters depth. Using this criterion the 2,000-decibar surface was selected for reference in the computation of dynamic heights.

Figure 40 shows the surface current situation found to exist during this survey. Because of the previously mentioned disposition of stations in the form of sections rather than in a close network, there was a greater than usual uncertainty regarding the exact course of the dynamic isobaths in the southeastern portion of the area surveyed. Consequently the isobaths have been shown as broken lines in the regions of greatest uncertainty. After careful consideration a tentative pattern of isobaths was selected and tested, where possible, by other criteria than density distribution. Thus the map is in accord with the direction of drift indicated by the wire angle at stations where light wind or calm weather prevailed, and with the set indicated by astronomical observations on runs between stations. The depth of the 10° isotherm, which Iselin [3] has found so convenient an indicator of the circulation in the western North Atlantic, was examined for those stations taken in or near the Atlantic Current. The numbers shown at the stations in figure 40 give the depth, in meters, of the 10° isotherm. An examination of these depths shows a notable correspondence between the contour lines of this thermal surface and the indicated course of the dynamic isobaths. Such a correspondence materially supports the current map as drawn.

---

[3] Iselin, C. O'D. A Study of the Circulation of the Western North Atlantic. Papers in Phys. Oceanog. and Met. M. I. T. and W. H. O. I., pp. 69–72, Vol. IV, No. 4, Cambridge, Mass., 1936.

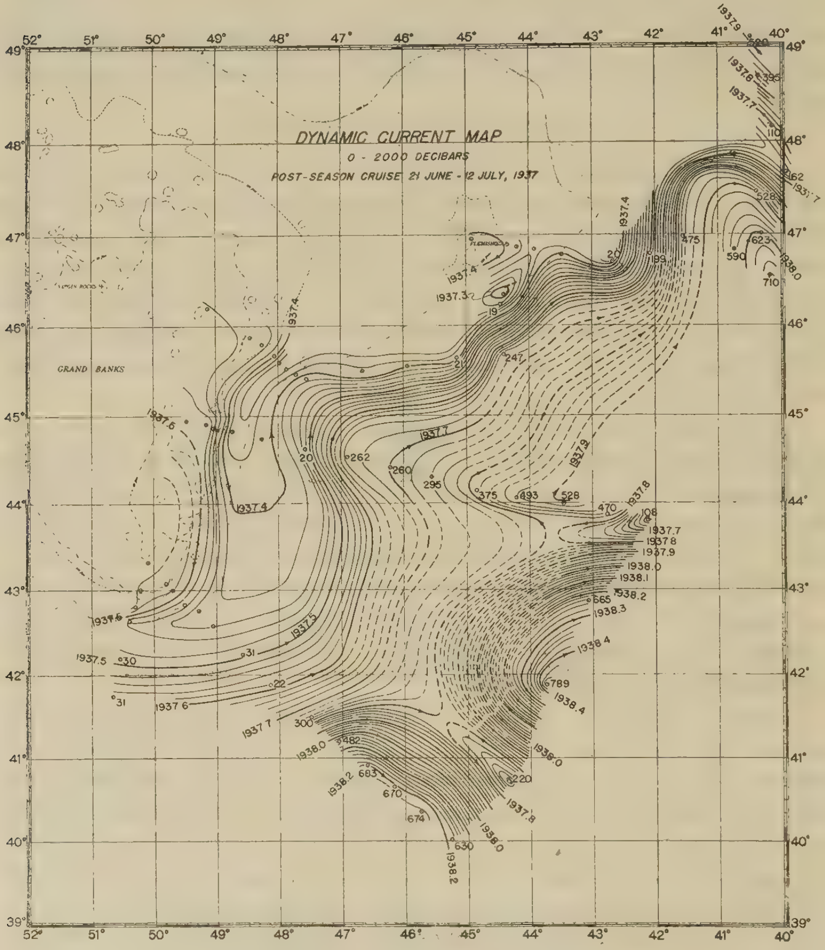

DYNAMIC CURRENT MAP
0 - 2000 DECIBARS
POST-SEASON CRUISE 21 JUNE - 12 JULY, 1937
GRAND BANKS
52°
51°
50°
49°
48°
47°
46°
45°
44°
43°
42°
41°
40°
39°
1937.4
1937.3
1937.5
1937.6
1937.7
1937.8
1937.9
1938.0
1938.1
1938.2
1938.3
1938.4
20
19
21
22
30
31
247
260
262
295
300
375
470
475
482
493
528
565
590
623
630
670
674
683
710
789
199
220
108
110
162
395
520

FIGURE 40.—Dynamic current map, from data collected on post-season cruise, June 21–July 12, 1937.

As was mentioned in the discussion of figure 39, the boundary between the waters having Atlantic Current and Labrador Current characteristics, practically all of the water at intermediate depths in the southeastern part of the area had a negative salinity anomaly during this survey. It was considered probable that this was the result of the presence of large quantities of mixed water from the Labrador Current. This view is in accord with figure 40, the relatively low dynamic heights at stations 2485 and 2488, and the shallow depth of the 10° isotherm at these stations. This emphasizes one of the most important implications of figure 40, namely that the area is one of great variation with respect to currents; and at the same time suggests that variations in the size of the major mixed-water pool or parts of this pool which may be detached may, acting as virtual obstructions, be partly responsible for the Gulf Stream system dividing into the several branches of the Atlantic Current after passing eastward of longitude 50° W. It would seem that the accumulation of a large quantity of mixed water east of the southern part of the Grand Banks is dependent, not only on an active supply of Labrador Current water, but also on the strength with which the Atlantic Current intrudes westward toward the Banks in about latitude 45° N., and thus restricts the northward flow of the mixed water. Evidently the abnormal growth of this pool of mixed water is one of the conditions responsible for the occasionally reported extra-southeasterly drift of bergs.

The southernmost branch of the Atlantic Current recurves southwestward shortly after passing eastward of the longitude of the Grand Banks. It was hoped that the section running southeasterly from the Grand Banks (stations 2471 to 2484) would cross the major portion of the Atlantic Current including this southernmost branch. However, it would seem from the isobaths of figure 40 and also from the depth of the 10° isotherm at stations 2481 and 2486 that this section did not extend far enough to the south to cross the branch that eventually recurves toward Bermuda. There is, of course, the possibility that this branch continued as far as station 2486 before recurving, and that that station was part way across the branch in question. Other evidence regarding this question will be considered in connection with the volumes of flow across the various sections of the survey.

At many of the stations between the Tail of the Grand Banks and Flemish Cap the observations extended to 4,000 meters. Although these stations are so widely spaced that it is not possible to deduce from them detailed patterns of circulation, they nevertheless afford the opportunity of studying the major features. Examination of the anomalies of dynamic height at levels below 2,000 decibars with reference to that surface indicated increasing relative velocities to 3,500 decibars and a decrease from 3,500 to 4,000 decibars. Figure 41 shows the dynamic topography of the 3,500 decibar surface relative to the 2,000 decibar surface in terms of anomaly of dynamic height, with the contour interval one dynamic centimeter. Similarly constructed deep-level current charts of the Labrador Sea, published in United States Coast Guard Bulletin No. 26 and based on the 1935 post-season cruise, showed the deep water of the Labrador Sea moving southward along the American side and being joined by a contribution from the eastward south of the end of Reykjanes Ridge. In figure 41 we see the continuation of this southward flow of the deep water past Flemish Cap and continuing as far as latitude 40° N., the southern limit of the survey. Most of the flow continues close in to the edge of the Grand Banks but some of it travels more directly southward along the forty-first meridian, being separated from the major portion by a whorl which is roughly concentric with the bathymetric depression at about 44° N., 42° W.

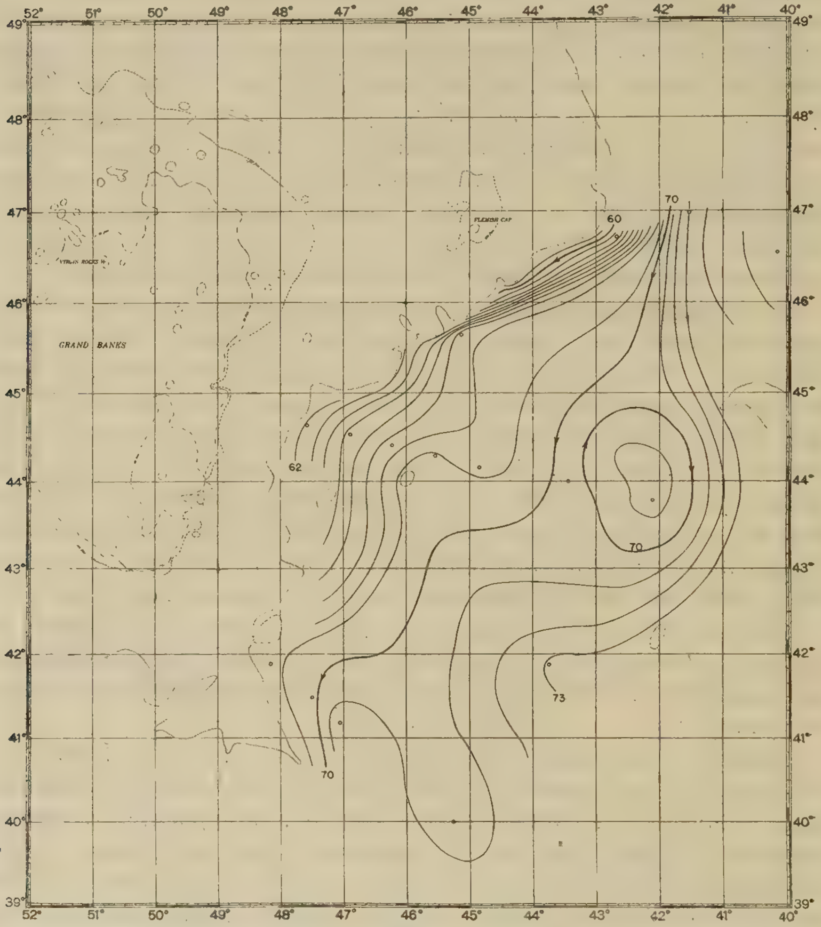


FIGURE 41.—Dynamic current map at 3,500 relative to 2,000 decibars. Isobaths represent differences in anomaly of dynamic height expressed in centimeters. From data collected on post-season cruise, June 21–July 12, 1937.

The criterion of least variability in horizontal gradients of anomaly of specific volume, which originally prompted the selection of the 2,000 decibar surface as a reference level, in itself means only the most nearly uniform velocity. It was assumed that this velocity was zero. Although such an assumption is considered reasonable, all available evidence must be considered. If some deeper level, such as the 3,500 decibar surface, is the most nearly motionless then the direction of flow at 2,000 decibars is opposite to that indicated by the arrows on figure 41. In either case the direction of flow will be along the dynamic isobaths shown. The temperature—salinity correlation was studied at each end of the area in question. All of the observations from depths greater than 1,500 meters from stations 2523 to 2528 east of Flemish Cap have been plotted in figure 42 and the individual station curves drawn. The two broken lines, separated by about 0.03°/°° salinity, represent approximately the range of observational error. A similar plot of temperature against salinity has been made in figure 43 for all observations from depths greater than 1,500 meters at stations 2475 to 2484 on the section running southeasterly from the Tail of the Grand Banks. Again the individual station curves have been drawn and the envelopes indicated by broken lines. The separation of the envelopes is again about the range of observational error except in the vicinity of about 2.75°, where the characteristic shape of the individual station curves require a lower-salinity hump. From figures 42 and 43 have been derived the mean curves shown in figure 44 and representing the temperature-salinity correlation for the two extreme edges of the survey, along the course of the current, for depths greater than 1,500 meters. From figure 44 it will be seen that the two correlation curves cross and that in the upper part of the figure the water off Flemish Cap is fresher than off the Tail of the Banks whereas in

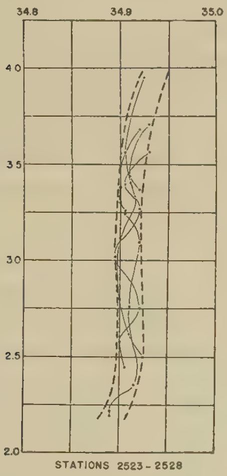


FIGURE 42.—Temperature-salinity correlation for all observations deeper than 1,500 meters at stations 2523–2528 occupied July 7–9, 1937, east of Flemish Cap.

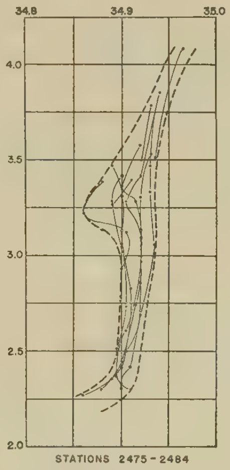


FIGURE 43.—Temperature-salinity correlation for all observations deeper than 1,500 meters at stations 2475–2484 occupied June 22–25, 1937, southeast of the Tail of the Grand Banks.

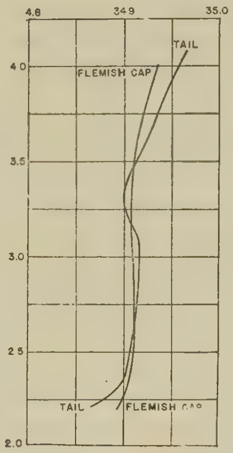


FIGURE 44.—Comparison of the temperature-salinity correlation for depths greater than 1,500 meters below the Atlantic Current east of Flemish Cap and southeast of the Tail of the Grand Banks.

the lower part of the figure, in the deeper water, that off the Tail of the Banks is fresher than that off Flemish Cap. If we consider that the source of this fresher water of more negative salinity anomaly is the downward mixing, cabbeling, mixed water containing Labrador Current water as a constituent and found all along the boundary between the Labrador and Atlantic Currents, then the interpretation is that in the upper levels the Atlantic Current is traveling from the Tail of the Banks toward Flemish Cap, and that in the deeper levels the water below the Atlantic Current is moving in the opposite direction, from Flemish Cap toward the Tail of the Grand Banks.

The corollary is that, at some level in between, the water is motionless and that the motionless level is at about where the two curves shown in figure 44 cross. The presence of the hump in the curve for the Tail of the Grand Banks makes it difficult to say from figure 44 where this motionless level is located more exactly than that it is between temperatures of about 2.7° and 3.4° which correspond to depths of about 1,750 and 3,200 meters respectively. Thus there is strong evidence in favor of the existence of a motionless surface such as was assumed in the construction of figure 41. Also, the assumed depth of this surface is within the limits indicated above from consideration of figure 44.

Another check on the assumption that the 2,000 decibar surface is most nearly motionless is made possible by the distribution of the isobaths in figure 41 with respect to the overlying Atlantic Current. The volume of flow of the Atlantic Current past the section east of Flemish Cap, determined by numerical computation and checked by planimeter measurements of a velocity profile, was 39.3 million cubic meters per second relative to the 2,000-decibar surface. Figure 41 indicates that the deep water velocity is greater at this section than in any other part of the survey. It should be mentioned here that accumulation of errors make the deep water velocity values less reliable than the values nearer the surface. However, it is believed that they are sufficiently accurate to furnish a significant check as to the direction of motion of the water between the 2,000 and 3,500-decibar surfaces. If, as was assumed in the construction of figure 41, the 2,000-decibar surface is motionless, the average velocity at the 3,500-decibar surface between stations 2523 and 2527 is 6.6 centimeters per second southerly and the average velocity of the water in the rectangular cross section between these two levels and these two stations is 3.3 centimeters per second southerly. However, if the 3,500-decibar surface is motionless the average velocity between these two stations is 6.6 centimeters per second northerly at the 2,000-decibar surface and the average velocity of the water in the previously mentioned rectangular cross section is 3.3 centimeters per second northerly and all of the velocities used in determining the volume of flow of the

Atlantic Current above 2,000 decibars between these two stations are too low by 6.6 centimeters per second, whence the volume of flow of the Atlantic Current past this section becomes 39.3 + 25.5 + 9.7, or 74.5 million cubic meters per second northerly.

An examination of figure 41 indicates that the deep water velocity past the section running southeasterly from the Tail of the Grand Banks is much less than it is east of Flemish Cap. Again taking the 2,000-decibar surface as motionless, the average velocity at the 3,500-decibar surface between stations 2478 and 2480 is 2.6 centimeters per second southerly whereas if the 3,500-decibar surface is motionless this represents the average northerly velocity between these two stations at the 2,000-decibar surface. If half this figure or 1.3 centimeters per second be taken as the average velocity of the water between the 2,000 and 3,500-decibar surfaces under the Atlantic Current at this section, the resulting volume of flow between these two surfaces and between stations 2475 and 2481 is about 5.9 million cubic meters per second, directed northerly if 3,500 decibars is the motionless surface and directed southerly if 2,000 decibars is the motionless surface. Furthermore, if the 3,500-decibar surface is motionless any determination of the volume of flow above 2,000 decibars relative to that surface will be based on velocities which are uniformly too low by 2.6 centimeters per second, which over the distance between stations 2475 and 2481 and from 0 to 2,000 decibars will result in a discrepancy of 15.8 million cubic meters per second. Thus if the 3,500-decibar surface is motionless, and if we assume that the Atlantic Current passing the Flemish Cap section is the same as the Atlantic Current passing the southern section, a determination of the volume of flow past the latter section from 0 to 2,000 decibars, relative to 2,000 decibars should be 74.5, 5.9, 15.8, or 52.8 million cubic meters per second; but if the 2,000-decibar surface is motionless, the result should be 39.3 million cubic meters per second.

Numerical computation, again checked by planimeter measurements of a velocity profile of the Atlantic Current past this southern section, actually showed a volume of flow of 42.8 million cubic meters per second, which is much nearer the figure of 39.3 than the alternate figure of 52.8. Thus it is considered that from another standpoint the 2,000-decibar surface is indicated to be more nearly motionless than the 3,500-decibar surface.

Attention must again be directed to some of the assumptions involved in the foregoing; namely, that the deep water velocities are sufficiently reliable to make the check significant, that the vertical distribution of the deep-water velocity is near enough to being linear for purposes of the check, and that the volume of flow of the Atlantic Current past the two sections is the same. Further consideration of the volumes of flow past the various sections shows the following, in which the units are million of cubic meters per second and the reference surface 2,000 decibars: between about stations 2481 and 2484 on the southern section, 7.4 southeasterly, joined by 25.2 southerly between stations 2484 and 2485 at the southern end of the contiguous section; 44.8 northwesterly between stations 2485 and 2486 with a flow of 52.3, determined by numerical computation alone, between stations 2475 and 2486; 49.1 easterly between stations 2486 and 2488, the latter station being the turning point between sections; 18.0 southwesterly between about stations 2488 and 2490 and 25.2 northerly between about stations 2490 and 2489, the western edge of the Atlantic Current past this section; 39.3 northerly between about stations 2523 and 2527 on the section eastward from Flemish Cap; 25.9 easterly between about stations 2527 and 2530; 14.3 westerly between about stations 2530 and 2533; 27.3 easterly between about stations 2533 and 2539; and 3.7 westerly between about stations 2539 and 2540, the northernmost station of the survey. These volumes of flow and their interrelation are shown schematically on figure 45 which is a sketch transport map in which each line represents approximately 5 million cubic meters per second volume of flow.

An inspection of figure 45 indicates that it is reasonable to make the assumption mentioned above, that the Atlantic Current passing the southern section also passes the section running east from Flemish Cap. Figure 45 is also in agreement with the results of the 1935 post-season cruise which indicated that the northernmost branch of the Atlantic Current extends to about latitude 55° N., before turning eastward. An examination of the temperature-salinity correlation at depths of from 400 to 1,000 meters at station 2486 indicated, as did the depth of the 10° isotherm, and the dynamic height, that that station had water of characteristics most nearly approaching those of Sargasso Sea water and was therefore farthest across the Atlantic Current of any station in the survey. A comparison of the temperature-salinity correlation at this station with those at the *Atlantis* stations along the meridianal section in about longitude 30° W., reported by Iselin [4] (1936) indicated that the water passing station 2486 was of similar character to that slightly north of *Atlantis* station 1014 and consequently was not only not a part of the branch of the Atlantic Current which recurves toward Bermuda, but that probably it was not all of the way across the part of the Atlantic Current which continues east, north of the Azores. A similar comparison of station 2486 with the temperature-salinity characteristics of another section running north from the Azores and reported on by Iselin [5] (1930) similarly indicated that the water at station 2486 crosses the Atlantic

---

[4] Loc. cit.

[5] Iselin, C. O. Recent work on the dynamic oceanography of the North Atlantic. Pub. Nation. Res. Council, Trans. Amer. Geophys. Union, tenth annual meeting, 82-89 (June, 1930) Washington.

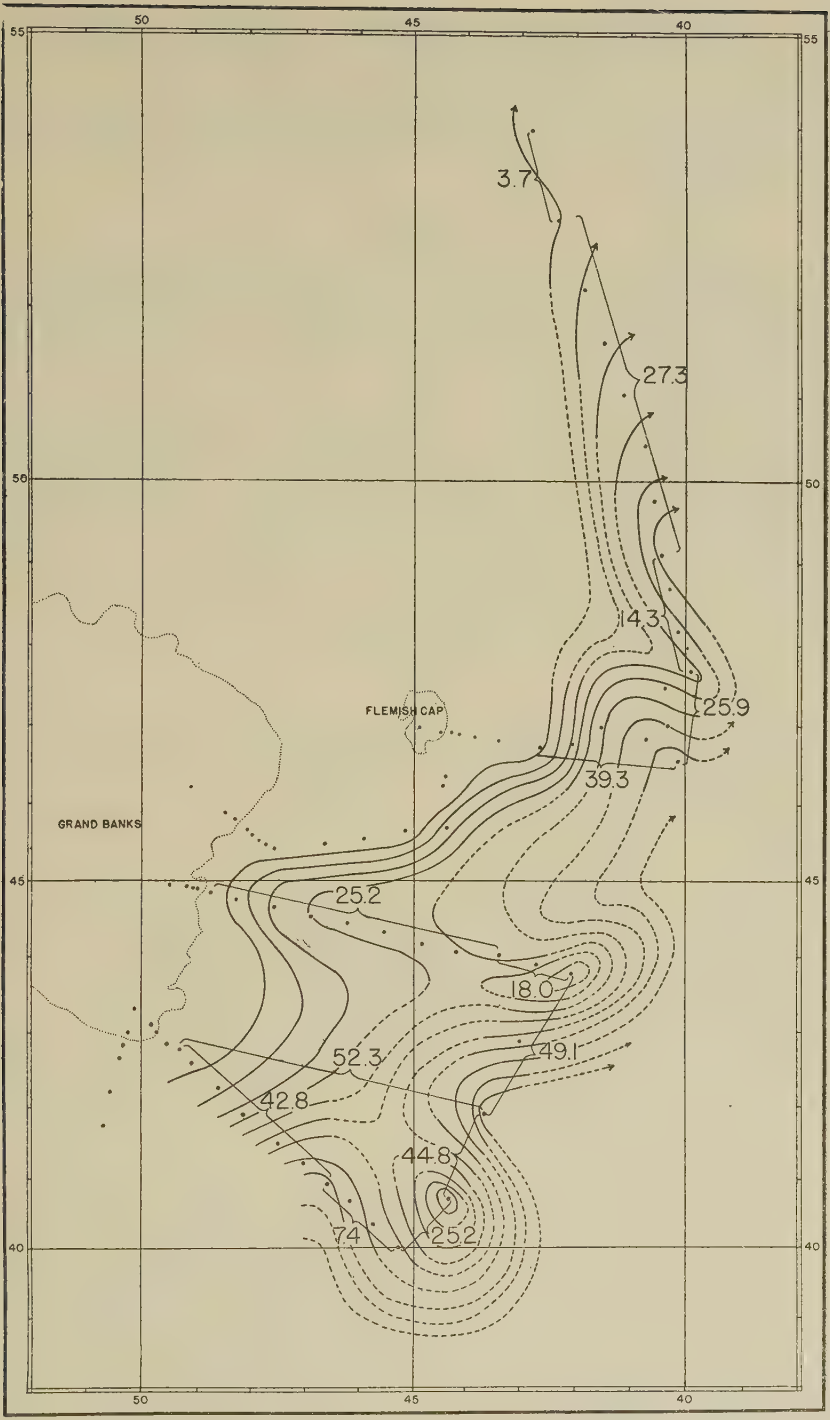

50
45
40
55
50
45
40
3.7
27.3
14.3
25.9
39.3
FLEMISH CAP
GRAND BANKS
25.2
18.0
49.1
52.3
42.8
44.8
74
25.2

FIGURE 45.—Schematic transport map showing the pattern of the Atlantic Current in the vicinity of the Grand Banks during the post-season cruise, June 21–July 12, 1937. Each streamline represents a volume of flow of approximately 5 million cubic meters per second.

north of the Azores and was comparable to that at about Iselin's station 231. Thus there is reason to believe that if the survey made on the 1937 post-season cruise had extended farther to the south and east we would have found additional current moving eastward across the Atlantic before we reached the branch or branches which recurve toward Bermuda.

SUMMARY

1. Three current surveys of the region immediately eastward of the Grand Banks were made during the 1937 ice season and an additional survey extending farther to the south, east, and north was made on a post-season cruise, and the current patterns found have been described.

2. The seasonal variation in the volume of flow of the Labrador Current during 1937 has been quantitatively determined and compared with conditions existing during the previous three ice seasons.

3. The volume of water contributed eastward across the Grand Banks by the western branch of the Labrador Current which flows southward along the Avalon Peninsula of Newfoundland was greater than usual during 1937 and has been discussed in relation to iceberg data and the flood of the West Greenland Current past Cape Farewell in 1935.

4. The boundary between Atlantic Current water and Labrador Current water, on the basis of the horizontal projection of the course of the zero salinity anomaly at the intermediate salinity anomaly maximum, has been shown with relation to the position of the 4-year average 1934–37.

5. The abnormally large quantity of mixed water found east of the Grand Banks during the 1937 post-season cruise indicated the great variability in current pattern to which this area is subject and has been considered with respect to extra-southerly berg-drifts.

6. Temperature-salinity curves representing conditions found on the post-season cruise have been compared with those from other observations north of the Azores and in the Sargasso Sea and indicate that the sections made on the post-season cruise did not completely cross the Atlantic Current.

7. The post-season cruise presents additional evidence that a most nearly motionless level exists, in the region surveyed, at a depth of about 2,000 or 2,500 meters; and that below this level the deep water is in motion in a direction counter to the overlying Atlantic Current.

It is evident that oceanic circulation in these areas is of fundamental importance in controlling the distribution of menacing ice. The results reported on here should be regarded as steps made toward the solution of the larger problem of this continuing investigation, rather than as entities complete in themselves.

In the following table are given the data collected during the 1937 season and post-season cruises. The individual station headings give the station number, date, geographical position, depth of water, and dynamic height of the sea surface above the reference surface used in the construction of the dynamic topographic charts shown in figures 34, 35, 36, and 40. For stations 2265 to 2465, inclusive, the sea surface is referred to the 1,000-decibar surface and the depth of water is the uncorrected fathometer sounding based on a sounding velocity of approximately 1,447 meters per second. For stations 2466 to 2540, inclusive, the sea surface is referred to the 2,000-decibar surface and the depth of water is the sonic sounding corrected for sounding velocity and draft but not for slope. Where the depths of the scaled values are enclosed in parentheses, the data are based on extrapolated vertical distribution curves of temperature, or salinity, or both. Asterisks appearing before observed temperatures indicate that these temperatures were determined from the depth of reversal and the corrected reading of an unprotected thermometer. The symbol σ_t signifies 1,000 (density −1).

TABLE OF OCEANOGRAPHIC DATA

STATIONS OCCUPIED IN 1937

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
Station 2265; Mar. 31; latitude 43°54′ N., longitude 53°54′ W.; depth 3,310 meters, dynamic height 971.116 meters						
0	10.77	34.86	0	10.77	34.86	26.72
26	10.71	34.86	25	10.70	34.86	26.74
51	10.71	34.86	50	10.70	34.86	26 74
77	10.71	34.86	75	10.70	34.86	26.74
103	10.72	34.86	100	10.70	34.86	26.74
154	12.32	35.47	150	12.30	35.46	26.91
205	10.51	35.28	200	10.75	35.29	27.06
308	7.67	35.00	300	7.85	35.01	27.33
355	6.58	34.90	400	6.05	34.91	27.50
546	5.05	34.97	600	4.85	34.97	27.69
750	4.44	34.98	800	4.35	34.98	27.75
940	4.12	34.99	1,000	4.05	34.99	27.79
1,338	3.69	34.97				
Station 2266; Mar. 31; latitude 43°56′ N., longitude 53°13′ W.; depth 2,853 meters, dynamic height 971.116 meters						
0	9.91	34.64	0	9.91	34.64	26.71
25	10.28	34.73	25	10.28	34.73	26.70
51	10.50	34.78	50	10.50	34.78	26.71
76	10.58	34.80	75	10.55	34.80	26.72
102	10.73	34.85	100	10.70	34.84	26.72
152	11.87	35.42	150	11.85	35.41	26.96
203	10.89	35.34	200	11.00	35.35	27.07
305	7.03	34.86	300	7.25	34.88	27.31
378	4.65	34.66	400	4.70	34.69	27.48
571	4.93	34.98	600	4.90	34.98	27.69
774	4.39	34.99	800	4.35	34.99	27.76
964	4.17	35.00	1,000	4.10	35.00	27 80
1,366	3.52	34.93				

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
Station 2267; Mar. 31; latitude 43°57′ N., longitude 52°50′ W.; depth 1,463 meters, dynamic height 971.060 meters						
0	2.16	32.72	0	2.16	32.72	26.16
25	1.27	32.67	25	1.26	32.67	26.18
51	1.05	32.70	50	1.05	32.69	26.21
76	3.44	33.19	75	3.40	33.18	26.42
102	4.52	33.98	100	4.40	33.90	26.89
153	5.88	34.52	150	5.85	34.50	27.20
204	5.50	34.64	200	5.55	34.63	27.33
306	4.45	34.74	300	4.50	34.74	27.54
382	4.23	34.80	400	4.25	34.81	27.63
577	4.40	34.95	600	4.35	34.95	27.73
780	4.07	34.94	800	4.00	34.94	27.76
971	3.82	34.94	1,000	3.80	34.94	27.78
1,369	3.58	34.94				
Station 2268; Apr. 8; latitude 43°57′ N., longitude 52°37′ W.; depth 622 meters; dynamic height 971.037 meters						
0	2.80	32.74	0	2.80	32.74	26.13
25	2.89	32.89	25	2.88	32.89	26.23
51	2.92	32.98	50	2.90	32.98	26.31
76	5.18	33.79	75	5.15	33.77	26.71
102	7.24	34.68	100	7.20	34.67	27.15
152	5.43	34.53	150	5.90	34.53	27.21
203	5.73	34.69	200	5.75	34.69	27.36
305	4.44	34.70	300	4.45	34.70	27.52
408	4.82	34.90	400	4.85	34.90	27.63
613	3.89	34.91	600	3.95	34.91	27.74

TABLE OF OCEANOGRAPHIC DATA—Continued

STATIONS OCCUPIED IN 1937—Continued

Station 2269; Apr. 1; latitude 43°58′ N., longitude 52°23′ W.; depth 167 meters; dynamic height 971.062 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	2.12	32.40	0	2.12	32.40	25.91
24	2.13	32.40	25	2.15	32.40	25.91
47	2.16	32.53	50	2.20	32.63	26.08
71	3.53	33.50	75	3.70	33.58	26.71
94	4.27	34.16	100	4.40	34.21	27.14
141	5.32	34.41	150	5.40	34.43	27.19

Station 2270; Apr. 1; latitude 43°59′ N., longitude 51°52′ W.; depth 89 meters; dynamic height 971.077 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	2.60	32.43	0	2.60	32.43	25.89
26	2.61	32.43	25	2.60	32.43	25.89
53	2.21	32.56	50	2.25	32.53	26.00
79	2.60	33.26	75	2.55	33.18	26.50

Station 2271; Apr. 1; latitude 44°00′ N., longitude 51°30′ W.; depth 77 meters; dynamic height 971.079 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	2.45	32.37	0	2.45	32.37	25.85
28	2.40	32.38	25	2.40	32.38	25.87
55	2.29	32.39	50	2.30	32.39	25.89
72	2.59	32.89	75	2.60	32.97	26.32

Station 2272; Apr. 1; latitude 43°56′ N., longitude 51°34′ W.; depth 84 meters; dynamic height 971.066 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	2.43	32.35	0	2.43	32.35	25.84
16	2.38	32.36	25	2.35	32.36	25.85
42	2.29	32.36	50	2.25	32.41	25.91
69	2.10	33.29	75	2.10	33.48	26.77

Station 2273; Apr. 1; latitude 43°34′ N.; longitude 51°54′ W.; depth 238 meters; dynamic height 971.023 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	2.87	32.76	0	2.87	32.76	26.16
26	4.64	33.36	25	4.60	33.35	26.42
52	4.50	33.70	50	4.50	33.67	26.70
78	6.03	34.36	75	6.05	34.36	27.06
104	4.53	34.34	100	4.80	34.34	27.19
156	3.49	34.25	150	3.55	34.25	27.26
208	3.53	34.30	200	3.50	34.29	27.29

Station 2274; Apr. 1; latitude 43°31′ N., longitude 51°58′ W.; depth 622 meters; dynamic height 971.010 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	2.64	32.72	0	2.64	32.72	26.12
25	4.11	33.35	25	4.11	33.35	26.48
51	4.70	33.85	50	4.70	33.84	26.81
76	5.58	34.29	75	5.60	34.29	27.06
101	3.81	34.18	100	3.85	34.18	27.17
152	3.95	34.35	150	3.90	34.34	27.29
203	4.49	34.52	200	4.50	34.51	27.37
304	3.78	34.60	300	3.80	34.60	27.51
393	3.86	34.77	400	3.90	34.78	27.64
590	3.98	34.89	600	4.00	34.89	27.72

Station 2275; Apr. 1; latitude 43°25′ N., longitude 52°05′ W.; depth 1,472 meters; dynamic height 971.018 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	3.31	32.97	0	3.31	32.97	26.26
26	3.20	32.98	25	3.20	32.98	26.28
52	4.82	33.37	50	4.50	33.32	26.41
77	7.10	34.48	75	6.95	34.44	27.00
103	8.26	34.90	100	8.25	34.89	27.17
155	7.30	34.90	150	7.50	34.90	27.29
207	5.29	34.67	200	5.40	34.68	27.39
310	5.25	34.88	300	5.25	34.87	27.57
387	3.67	34.75	400	3.70	34.75	27.64
592	4.07	34.90	600	4.05	34.90	27.72
845	3.99	34.94	800	4.00	34.94	27.76
1,003	3.84	34.94	1,000	3.85	34.94	27.77
1,402	3.55	34.93				

Station 2276; Apr. 1; latitude 43°01′ N., longitude 52°34′ W.; depth 3,941 meters; dynamic height 971.106 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	5.72	33.60	0	5.72	33.60	26.51
22	8.38	34.27	25	8.40	34.27	26.66
44	8.54	34.31	50	8.60	34.35	26.69
66		34.48	75	8.95	34.58	26.81
88	*9.05	34.69	100	9.15	34.83	26.98
132		35.13	150	9.25	35.19	27.24
175	*9.26	35.22	200	8.80	35.15	27.29
263	7.67	34.94	300	7.35	34.90	27.31
363	7.11	34.78	400	6.05	34.76	27.38
464	4.89	34.74	600	3.85	34.78	27.64
548	3.72	34.74	800	4.05	34.92	27.74
656	3.93	34.84	1,000	4.00	34.95	27.77
962	4.02	34.95				

Station 2277; Apr. 2; latitude 42°37′ N., longitude 53°03′ W.; depth 4,170 meters; dynamic height 971.103 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	6.50	33.75	0	6.50	33.75	26.52
24	8.88	34.38	25	8.90	34.39	26.67
47	9.57	34.56	50	9.60	34.57	26.71
71	9.61	34.58	75	9.65	34.59	26.71
94	10.04	34.71	100	10.20	34.79	26.77
141	11.45	35.26	150	11.25	35.24	26.94
188	9.63	35.10	200	8.90	35.04	27.18
282	4.32	34.48	300	4.60	34.58	27.40
298	5.40	34.67	400	3.40	34.57	27.53
463	3.18	34.59	600	3.90	34.80	27.66
680	4.22	34.89	800	4.05	34.90	27.72
820	4.02	34.90	1,000	3.90	34.92	27.76
1,205	3.80	34.94				

Station 2278; Apr. 2; latitude 42°19′ N., longitude 52°31′ W.; depth 4,051 meters; dynamic height 971.063 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	5.00	33.48	0	5.00	33.48	26.49
20	5.01	33.48	25	5.05	33.48	26.48
39	5.19	33.52	50	5.70	33.60	26.51
59	5.91	33.67	75	5.60	33.78	26.66
79	5.52	33.81	100	5.05	33.99	26.89
118	4.92	34.12	150	5.05	34.33	27.16
157	5.08	34.37	200	5.20	34.56	27.33
236	4.37	34.50	300	4.35	34.63	27.47
213	5.17	34.60	400	4.25	34.75	27.58
334	4.34	34.68	600	4.25	34.90	27.70
501	4.10	34.82	800	4.15	34.94	27.74
610	4.25	34.91	1,000	3.85	34.94	27.77
931	3.92	34.94				

TABLE OF OCEANOGRAPHIC DATA—Continued

STATIONS OCCUPIED IN 1937—Continued

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
Station 2279; Apr. 2; latitude 42°04′ N., longitude 52°06′ W.; depth 3,484 meters; dynamic height 971.033 meters						
0	3.54	33.05	0	3.54	33.05	26.30
25	3.55	33.06	25	3.55	33.06	26.30
49	7.54	34.04	50	7.50	34.04	26.61
74	5.99	34.04	75	6.00	34.04	26.81
98	7.90	35.04	100	9.00	35.04	27.17
147	8.48	34.93	150	8.45	34.93	27.17
195	8.43	35.02	200	8.40	35.02	27.25
293	4.60	34.72	300	4.35	34.70	27.53
310	3.89	34.69	400	4.25	34.80	27.62
471	4.34	34.88	600	4.35	34.95	27.73
635	4.31	34.96	800	4.05	34.98	27.78
815	4.01	34.98	1,000	3.80	34.96	27.80
1,247	3.56	34.94				
Station 2280; Apr. 2; latitude 42°18′ N., longitude 51°44′ W.; depth 3,557 meters; dynamic height 970.981 meters						
0	4.29	33.45	0	4.29	33.45	26.55
24	4.30	33.46	25	4.30	33.47	26.57
46	4.57	33.88	50	4.55	33.88	26.85
70	4.38	33.97	75	4.30	33.98	26.96
93	4.11	34.06	100	4.10	34.09	27.07
139	4.40	34.32	150	4.90	34.42	27.25
185	6.38	34.79	200	6.10	34.80	27.40
278	4.88	34.81	300	4.80	34.83	27.58
317	4.70	34.84	400	4.65	34.92	27.68
495	4.53	34.98	600	4.25	34.98	27.76
687	4.06	34.97	800	3.90	34.96	27.79
876	3.83	34.96	(1,000)	3.75	34.95	27.79
Station 2281; Apr. 2–3; latitude 42°31′ N., longitude 51°23′ W.; depth 2,752 meters; dynamic height 970.987 meters						
0	3.75	33.57	0	3.76	33.57	26.70
28	3.77	33.58	25	3.75	33.58	26.70
55	4.39	33.90	50	4.35	33.83	26.83
82	3.70	33.98	75	3.90	33.96	26.99
109	3.37	34.11	100	3.45	34.07	27.12
164	3.28	34.29	150	3.30	34.27	27.30
219	2.34	34.39	200	2.55	34.30	27.39
328	4.23	34.76	300	3.95	34.66	27.54
656	4.37	34.97	400	4.35	34.86	27.66
955	3.82	34.96	600	4.40	34.96	27.73
1,078	3.59	34.94	800	4.15	34.97	27.77
1,249	3.48	34.94	1,000	3.75	34.95	27.79
Station 2282; Apr. 3; latitude 42°48′ N., longitude 50°58′ W.; depth 1,920 meters; dynamic height 970.974 meters						
0	0.12	33.32	0	0.12	33.32	26.76
24	.11	33.32	25	.11	33.32	26.77
48	.25	-------	50	.30	33.50	26.90
72	1.40	33.72	75	1.40	33.72	27.01
96	.10	33.74	100	.10	33.76	27.12
144	1.28	34.00	150	1.50	34.03	27.25
192	2.43	34.24	200	2.50	34.26	27.36
288	2.94	34.53	300	3.00	34.57	27.57
372	3.58	34.75	400	3.70	34.79	27.67
561	3.84	34.90	600	3.85	34.91	27.75
750	3.79	34.92	800	3.75	34.92	27.77
988	3.68	34.94	1,000	3.70	34.94	27.79
1,582	3.44	34.93				

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
Station 2283; Apr. 3; latitude 42°57′ N., longitude 50°43′ W.; depth 622 meters; dynamic height 971.024 meters						
0	0.93	33.36	0	0.93	33.36	26.75
30	.83	33.33	25	.90	33.34	26.74
60	—.19	33.32	50	0.00	33.32	26.77
89	—.19	33.52	75	—.20	33.41	26.86
118	—.11	33.63	100	—.15	33.57	26.99
177	.74	33.86	150	.40	33.76	27.11
237	1.27	34.04	200	.95	33.93	27.20
355	3.51	34.64	300	2.05	34.25	27.39
335	2.72	34.37	400	3.70	34.74	27.63
563	3.85	34.89	600	3.85	34.91	27.75
Station 2284; Apr. 3; latitude 43°07′ N., longitude 50°30′ W.; depth 88 meters; dynamic height 971.037 meters						
0	2.24	33.42	0	2.24	33.42	26.72
30	2.19	33.42	25	2.20	33.42	26.72
59	2.72	33.58	50	2.55	33.52	26.77
89	3.53	33.83	75	3.15	33.72	26.87
Station 2285; Apr. 3; latitude 43°22′ N., longitude 50°08′ W.; depth 66 meters; dynamic height 971.037 meters						
0	1.49	33.24	0	1.49	33.24	26.62
28	1.54	33.28	25	1.55	33.28	26.65
57	1.53	33.28	50	1.50	33.28	26.65
Station 2286; Apr. 3; latitude 43°00′ N., longitude 50°08′ W.; depth 88 meters; dynamic height 971.024 meters						
0	1.13	33.28	0	1.13	33.28	26.68
19	1.14	33.28	25	1.14	33.28	26.68
45	1.20	33.30	50	1.25	33.34	26.71
71	1.88	33.59	75	2.00	33.66	26.92
Station 2287; Apr. 3; latitude 42°48′ N., longitude 50°08′ W.; depth 686 meters; dynamic height 971.006 meters						
0	0.55	33.22	0	0.55	33.22	26.66
23	.53	33.22	25	.50	33.22	26.66
47	.13	33.32	50	.10	33.34	26.79
70	—.18	33.43	75	—.20	33.45	26.89
93	—.29	33.56	100	—.30	33.58	26.99
140	—.08	33.67	150	0.00	33.70	27.08
187	.37	33.82	200	.50	33.88	27.19
280	1.61	34.12	300	2.90	34.56	27.57
300	3.10	34.59	400	3.70	34.81	27.69
462	3.88	34.88	(600)	3.85	34.91	27.75

TABLE OF OCEANOGRAPHIC DATA—Continued

STATIONS OCCUPIED IN 1937—Continued

Station 2288; Apr. 4; latitude 42°30′ N., longitude 50°08′ W.; depth 2,424 meters: dynamic height 970.994 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	0.19	33.32	0	0.19	33.32	26.76
26	.19	33.32	25	.20	33.32	26.76
51	−.08	33.33	50	−.05	33.33	26.78
77	.79	33.60	75	.75	33.59	26.95
103	1.57	33.84	100	1.40	33.81	27.08
154	4.06	34.32	150	3.90	34.31	27.27
205	3.04	34.32	200	3.10	34.32	27.36
308	3.71	34.65	300	3.70	34.63	27.54
404	3.81	34.78	400	3.80	34.77	27.65
607	4.35	34.96	600	4.35	34.95	27.73
810	4.22	34.99	800	4.25	34.99	27.77
1,012	3.95	34.98	1,000	3.95	34.98	27.79
1,416	3.60	34.95				

Station 2289; Apr. 4; latitude 42°00′ N., longitude 50°08′ W.; depth 2,603 meters; dynamic height 971.081 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	4.08	33.17	0	4.08	33.17	26.34
25	4.08	33.18	25	4.08	33.18	26.35
50	5.14	33.57	50	5.14	33.57	26.55
75	7.74	34.28	75	7.74	34.28	26.76
100	7.36	34.29	100	7.36	34.29	26.83
150	5.33	34.26	150	5.33	34.26	27.07
201	7.88	34.85	200	7.85	34.84	27.19
301	6.94	34.96	300	7.00	34.96	27.41
368	4.87	34.80	400	4.85	34.82	27.57
562	4.86	35.00	600	4.80	35.00	27.72
761	4.20	34.98	800	4.15	34.98	27.77
963	3.96	34.96	1,000	3.90	34.96	27.79
1,381	3.52	34.94				

Station 2290; Apr. 4; latitude 41°40′ N., longitude 49°20′ W.; depth 2,770 meters; dynamic height 971.066 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	6.37	33.92	0	6.37	33.92	26.68
24	6.70	33.90	25	6.70	33.90	26.61
48	6.35	33.93	50	6.40	33.96	26.70
71	8.55	34.42	75	9.05	34.48	26.72
95	10.44	34.84	100	10.55	34.89	26.79
142	10.80	35.20	150	10.75	35.20	27.00
190	9.26	35.04	200	8.95	35.01	27.16
285	6.89	34.89	300	7.20	34.99	27.40
304	7.28	35.01	400	6.00	35.02	27.59
472	5.39	35.02	600	4.75	35.02	27.74
651	4.51	35.02	800	4.05	35.00	27.80
844	4.00	34.99	1,000	3.85	34.98	27.80
1,396	3.15	34.96				

Station 2291; Apr. 6; latitude 41°56′ N., longitude 46°59′ W.; depth 4,335 meters; dynamic height 971.275 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	13.21	35.32	0	13.21	35.32	26.62
24	13.29	35.32	25	13.39	35.32	26.60
48	13.28	35.31	50	13.30	35.32	26.60
72	13.29	35.32	75	13.30	35.32	26.60
96	13.28	35.32	100	13.30	35.32	26.60
144	13.29	35.31	150	13.25	35.32	26.61
193	12.91	35.55	200	12.85	35.54	26.86
289	10.71	35.36	300	10.65	35.35	27.13
480	10.42	35.32	400	10.55	35.34	27.14
551	7.18	35.06	600	6.50	35.05	27.55
668	5.70	35.05	800	4.60	34.99	27.73
846	4.39	34.98	1,000	4.10	34.98	27.78
1,347	3.74	34.98				

Station 2292; Apr. 6; latitude 42°10′ N., longitude 47°40′ W.; depth 3,612 meters; dynamic height 971.094 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	9.99	34.57	0	9.99	34.57	26.64
25	9.98	34.55	25	9.98	34.55	26.62
51	10.00	34.52	50	10.00	34.52	26.60
76	9.79	34.50	75	9.80	34.50	26.61
101	9.51	34.51	100	9.35	34.51	26.70
152	9.96	35.05	150	9.95	35.03	27.00
203	9.95	35.23	200	9.95	35.23	27.16
307	7.09	34.99	300	7.15	35.00	27.42
362	6.04	34.96	400	5.55	34.94	27.58
559	4.46	34.90	600	4.35	34.90	27.69
768	4.08	34.94	800	4.00	34.92	27.75
960	3.88	34.94	1,000	3.85	34.92	27.76
1,485	3.50	34.92				

Station 2293; Apr. 6–7; latitude 42°20′ N., longitude 48°27′ W.; depth 2,999 meters; dynamic height 971.011 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	9.91	34.60	0	9.91	34.60	26.68
25	9.95	34.60	25	9.95	34.60	26.67
50	9.93	34.60	50	9.95	34.60	26.67
76	9.16	34.53	75	9.20	34.54	26.74
101	4.89	34.13	100	4.95	34.13	27.01
151	6.26	34.63	150	6.25	34.61	27.23
202	7.51	35.02	200	7.50	35.02	27.38
303	4.20	34.72	300	4.25	34.73	27.56
386	5.05	34.92	400	5.00	34.93	27.64
560	4.69	34.98	600	4.65	34.99	27.73
723	4.39	35.00	800	4.15	34.98	27.77
908	3.78	34.94	1,000	3.70	34.94	27.79
1,414	3.43	34.92				

Station 2294; Apr. 7; latitude 42°35′ N.; longitude 49°24′ W.; depth 2,112 meters; dynamic height 970.885 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	2.60	33.82	0	2.61	33.82	27.00
25	2.63	33.84	25	2.63	33.84	27.01
50	2.40	33.89	50	2.40	33.89	27.07
74	3.19	34.12	75	3.20	34.13	27.19
99	3.82	34.47	100	3.85	34.48	27.41
149	4.47	34.74	150	4.50	34.74	27.54
198	4.96	34.93	200	4.95	34.93	27.64
297	3.94	34.86	300	3.90	34.86	27.71
392	*3.82	34.90	400	3.80	34.90	27.75
589	3.82	34.92	600	3.80	34.92	27.77
788	3.68	34.92	800	3.65	34.92	27.78
976	3.64	34.92	1,000	3.60	34.92	27.79
1,491	3.46	34.92				

Station 2295; Apr. 7; latitude 43°32′ N., longitude 49°07′ W.; depth 1,563 meters; dynamic height 970.958 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	2.45	33.81	0	2.45	33.81	27.00
26	2.54	33.83	25	2.55	33.83	27.01
51	2.68	33.84	50	2.65	33.84	27.01
77	2.07	33.84	75	2.10	33.84	27.05
102	1.76	33.89	100	1.75	33.88	27.11
153	3.65	34.29	150	3.65	34.27	27.27
205	3.45	34.52	200	3.50	34.51	27.47
307	3.29	34.68	300	3.30	34.67	27.62
402	*2.12	34.72	400	3.15	34.72	27.67
603	3.73	34.88	600	3.75	34.88	27.73
805	3.73	34.90	800	3.75	34.90	27.75
1,004	3.68	34.91	1,000	3.70	34.91	27.77
1,402	3.70	34.91				

TABLE OF OCEANOGRAPHIC DATA—Continued

STATIONS OCCUPIED IN 1937—Continued

Station 2296; Apr. 7; latitude 43°13′ N., longitude 48°22′ W.; depth 2,241 meters; dynamic height 970.932 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	4.27	33.68	0	4.27	33.68	26.73
25	4.15	33.69	25	4.15	33.69	26.75
51	4.11	33.68	50	4.10	33.68	26.75
76	3.60	34.00	75	3.65	34.00	27.05
102	2.66	34.15	100	2.70	34.13	27.23
153	4.13	34.61	150	4.10	34.60	27.48
204	3.56	34.65	200	3.60	34.65	27.57
306	3.42	34.73	300	3.40	34.73	27.65
379	3.93	34.86	400	4.00	34.88	27.71
569	4.08	34.95	600	4.05	34.95	27.76
760	3.80	34.94	800	3.75	34.94	27.78
947	3.63	34.94	1,000	3.60	34.94	27.80
1,453	3.35	34.92				

Station 2297; Apr. 7; latitude 43°04′ N., longitude 47°38′ W.; depth 3,246 meters; dynamic height 970.987 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	7.65	34.49	0	7.65	34.49	26.94
25	7.70	34.50	25	7.70	34.50	26.94
51	7.65	34.48	50	7.65	34.48	26.93
76	7.25	34.43	75	7.25	34.43	26.95
101	7.20	34.46	100	7.20	34.46	26.99
152	7.40	34.82	150	7.40	34.81	27.23
203	6.94	34.88	200	7.00	34.88	27.34
304	4.80	34.76	300	4.90	34.76	27.52
424	3.35	34.76	400	3.45	34.76	27.67
628	4.26	34.96	600	4.20	34.95	27.75
830	3.91	34.95	800	4.00	34.95	27.77
1,022	3.63	34.93	1,000	3.65	34.93	27.78
1,537	3.34	34.92				

Station 2298; Apr. 8; latitude 42°56′ N., longitude 46°50° W.; depth 3,612 meters; dynamic height 971.099 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	11.64	34.94	0	11.64	34.94	26.63
24	11.63	34.94	25	11.65	34.94	26.63
48	11.60	34.91	50	11.60	34.91	26.62
72	11.65	34.94	75	11.65	34.94	26.63
96	11.66	34.94	100	11.70	34.95	26.63
144	12.29	35.47	150	12.25	35.47	26.93
192	10.39	35.28	200	10.00	35.25	27.16
288	7.23	34.94	300	6.95	34.92	27.39
364	7.61	34.97	400	4.90	34.83	27.57
406	4.81	34.83	600	3.25	34.77	27.70
553	3.11	34.72	800	3.90	34.90	27.74
700	3.95	34.90	1,000	3.75	34.91	27.76
1,123	3.65	34.91				

Station 2299; Apr. 8; latitude 43°23′ N., longitude 46°33′ W.; depth 3,969 meters; dynamic height 970.963 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	4.72	34.02	0	4.72	34.02	26.95
25	4.86	34.05	25	4.86	34.05	26.96
51	5.63	34.10	50	5.60	34.10	26.91
76	4.90	34.10	75	4.90	34.10	26.99
101	4.29	34.21	100	4.30	34.20	27.14
152	6.39	34.75	150	6.35	34.75	27.33
203	5.34	34.76	200	5.40	34.76	27.46
304	5.03	34.84	300	5.05	34.83	27.55
406	4.96	34.96	400	4.95	34.95	27.66
608	4.51	34.98	600	4.55	34.98	27.73
810	3.87	34.95	800	3.90	34.95	27.78
1,007	3.69	34.94	1,000	3.70	34.94	27.79
1,516	3.36	34.92				

Station 2300; Apr. 8; latitude 43°52′ N., longitude 46°17′ W.; depth 3,026 meters; dynamic height 971.080 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	11.51	35.39	0	11.51	35.39	27.00
26	11.50	35.39	25	11.50	35.39	27.00
52	11.50	35.40	50	11.50	35.40	27.01
79	11.51	35.40	75	11.50	35.40	27.01
105	11.53	35.41	100	11.55	35.41	27.01
157	11.53	35.44	150	11.55	35.44	27.03
209	10.90	35.36	200	11.05	35.38	27.07
314	8.21	35.07	300	8.60	35.11	27.29
380	6.66	34.98	400	6.35	34.98	27.51
574	4.89	34.97	600	4.80	34.97	27.70
770	4.27	34.96	800	4.20	34.96	27.76
955	3.97	34.945	1,000	3.95	34.94	27.76
1,466	3.52	34.935				

Station 2301; Apr. 8; latitude 43°59′ N., longitude 46°55′ W.; depth 4,079 meters dynamic height 971.158 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	11.37	35.30	0	11.37	35.30	26.96
25	11.36	35.31	25	11.36	35.31	26.97
50	11.36	35.31	50	11.36	35.31	26.97
75	11.35	35.31	75	11.36	35.31	26.97
100	11.33	35.31	100	11.33	35.31	26.97
150	11.36	35.31	150	11.36	35.31	26.97
201	11.36	35.31	200	11.35	35.31	26.97
301	9.32	35.01	300	9.35	35.02	27.10
349	7.52	34.81	400	7.00	34.86	27.33
536	5.97	34.98	600	5.45	34.98	27.62
732	4.64	34.98	800	4.40	34.98	27.74
917	4.15	34.98	1,000	4.05	34.98	27.78
1,432	3.56	34.94				

Station 2302; Apr. 8; latitude 44°11′ N.; longitude 47°45′ W.; depth 3,859 meters; dynamic height 971.047 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	10.88	35.24	0	10.88	35.24	27.00
22	10.90	35.24	25	10.90	35.24	27.00
44	10.88	35.24	50	10.90	35.24	27.00
65	10.88	35.24	75	10.85	35.23	27.00
87	10.82	35.22	100	10.85	35.23	27.00
131	10.93	35.26	150	10.85	35.26	27.02
175	10.58	35.25	200	9.85	35.20	27.15
262	8.49	35.06	300	8.00	35.08	27.35
298	8.07	35.08	400	6.15	34.98	27.53
444	5.46	34.96	600	4.50	34.99	27.74
588	4.59	34.99	800	3.90	34.96	27.79
746	4.01	34.96	1,000	3.70	34.94	27.79
1,207	3.53	34.93				

Station 2303; Apr. 9; latitude 44°23′ N., longitude 48°21′ W.; depth 3,155 meters; dynamic height 970.957 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	7.34	34.47	0	7.34	34.47	26.98
26	7.36	34.47	25	7.35	34.47	26.98
52	7.38	34.48	50	7.40	34.48	26.97
77	7.41	34.46	75	7.40	34.46	26.96
103	6.26	34.42	100	6.30	34.42	27.08
155	5.93	34.62	150	6.00	34.61	27.27
207	4.51	34.60	200	4.60	34.60	27.42
310	5.02	34.86	300	5.00	34.83	27.56
338	4.98	34.94	400	4.70	34.96	27.70
512	4.26	34.96	600	4.10	34.96	27.77
690	4.00	34.96	800	3.80	34.95	27.79
871	3.72	34.94	1,000	3.65	34.94	27.79
1,399	3.39	34.94				

TABLE OF OCEANOGRAPHIC DATA—Continued

STATIONS OCCUPIED IN 1937—Continued

Station 23.04; Apr. 9; latitude 44°23′ N.; longitude 48°47′ W.; depth 1,445 meters, dynamic height 970.939 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	−1.15	33.18	0	−1.15	33.18	26.70
26	−.44	33.45	25	−.45	33.44	26.89
51	2.58	33.92	50	2.50	33.88	27.05
77	4.98	34.30	75	4.90	34.29	27.14
103	5.06	34.34	100	5.05	34.33	27.16
154	3.84	34.39	150	3.85	34.39	27.34
206	4.04	34.58	200	4.05	34.56	27.45
309	2.76	34.64	300	2.80	34.63	27.62
403	3.24	34.78	400	3.25	34.78	27.70
608	3.64	34.89	600	3.65	34.89	27.75
815	3.61	34.92	800	3.60	34.92	27.79
1,017	3.56	34.93	1,000	3.55	34.93	27.79
1,417	3.53	34.93				

Station 2305; Apr. 9; latitude 44°21′ N., longitude 48°55′ W.; depth 622 meters; dynamic height 971.005 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	−1.25	33.17	0	−1.25	33.17	26.70
26	−1.27	33.18	25	−1.25	33.18	26.70
52	−1.27	33.24	50	−1.25	33.22	26.74
77	−1.31	33.52	75	−1.30	33.51	26.98
103	−.78	33.68	100	−.95	33.66	27.09
155	.30	33.88	150	.20	33.86	27.20
207	.90	34.02	200	.85	34.00	27.27
310	2.10	34.32	300	2.00	34.30	27.43
403	2.57	34.56	400	2.55	34.55	27.59
605	3.36	34.80	600	2.95	34.80	27.75

Station 2306; Apr. 9; latitude 44°19′ N.; longitude 49°06′ W.; depth 192 to 201 meters; dynamic height 971.051 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	−1.11	33.22	0	−1.11	33.22	26.73
26	−1.06	33.46	25	−1.05	33.46	26.93
53	−.91	33.51	50	−.90	33.50	26.96
79	−.93	33.53	75	−.90	33.53	26.98
106	−.84	33.56	100	−.85	33.55	26.99
158	−.79	33.60	150	−.80	33.60	27.03
190	−.72	33.63	200	−.70	33.64	27.06

Station 2307; Apr. 9; latitude 44°19′ N., longitude 49°09′ W.; depth 82 meters; dynamic height 971.061 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	−1.06	33.20	0	−1.06	33.20	26.72
26	−1.10	33.21	25	−1.10	33.21	26.73
52	−.91	33.45	50	−.90	33.44	26.91
78	−.91	33.44	75	−.90	33.44	26.91

Station 2308; Apr. 9; latitude 44°19′ N., longitude 49°41′ W.; depth 50 meters; dynamic height 971.068 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	0.54	33.21	0	0.54	33.21	26.66
22	.45	33.23	25	.45	33.23	26.68
44	.35	33.22	50	.30	33.22	26.68

Station 2309; Apr. 9; latitude 45°00′ N., longitude 49°37′ W.; depth 68 meters; dynamic height 971.046 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	−0.44	33.25	0	−0.44	33.25	26.73
28	−.44	33.25	25	−.45	33.25	26.73
56	−.59	33.26	50	−.55	33.26	26.74

Station 2310; Apr. 10; latitude 44°55′ N., longitude 49°14′ W.; depth 146 meters; dynamic height 971.041 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	−1.08	33.17	0	−1.08	33.17	26.69
26	−.95	33.31	25	−.95	33.30	26.79
53	−.90	33.36	50	−.90	33.36	26.84
79	−.99	33.37	75	−.95	33.37	26.85
106	−1.02	33.38	100	−1.00	33.38	26.86
143	−.86	33.54	(150)	−.80	33.57	27.01

Station 2311; Apr. 10; latitude 44°53′ N., longitude 49°09′ W.; depth 622 meters; dynamic height 971.009 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	−1.15	33.13	0	−1.15	33.13	26.66
26	−1.29	33.21	25	−1.30	33.21	26.73
51	−1.07	33.46	50	−1.05	33.45	26.92
77	−.86	33.53	75	−.85	33.52	26.97
102	−.29	33.76	100	−.35	33.74	27.12
153	.12	33.85	150	.10	33.85	27.19
205	.95	34.03	200	.85	34.02	27.29
307	1.65	34.22	300	1.60	34.21	27.39
391	*2.16	34.44	400	2.20	34.46	27.55
586	3.59	34.88	600	3.65	34.90	27.76

Station 2312; Apr. 10; latitude 44°46′ N., longitude 48°43′ W.; depth 1,463 to 1,792 meters; dynamic height 970.938 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	−0.66	33.21	0	−0.66	33.21	26.72
26	−.88	33.36	25	−.85	33.35	26.82
51	4.00	34.11	50	3.85	34.11	27.12
77	5.07	34.30	75	5.05	34.30	27.14
103	3.41	34.14	100	3.75	34.16	27.17
154	1.53	34.07	150	1.55	34.07	27.28
205	1.88	34.32	200	1.80	34.29	27.44
308	3.00	34.69	300	2.95	34.68	27.65
404	3.42	34.81	400	3.40	34.81	27.72
606	3.66	34.89	600	3.65	34.89	27.75
808	3.63	34.92	800	3.65	34.92	27.78
1,009	3.54	34.92	1,000	3.55	34.92	27.79
1,411	3.47	34.92				

Station 2313; Apr. 10; latitude 44°23′ N., longitude 48°12′ W.; depth 3,301 meters; dynamic height 970.912 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	3.44	33.95	0	3.44	33.95	27.02
25	4.44	34.20	25	4.44	34.20	27.12
50	4.83	34.28	50	4.83	34.28	27.14
75	4.68	34.30	75	4.68	34.30	27.17
100	3.91	34.23	100	3.91	34.23	27.20
150	4.40	34.40	150	4.40	34.40	27.29
200	4.26	34.67	200	4.26	34.67	27.52
300	3.21	34.74	300	3.21	34.74	27.68
237	4.33	34.76	400	4.20	34.94	27.74
365	4.29	34.94	600	3.80	34.93	27.74
500	3.87	34.92	800	3.70	34.93	27.78
648	3.77	34.93	1,000	3.50	34.93	27.80
1,084	3.46	34.93				

TABLE OF OCEANOGRAPHIC DATA—Continued

STATIONS OCCUPIED IN 1937—Continued

Station 2314; Apr. 10; latitude 44°35′ N., longitude 47°37′ W.; depth 3,621 meters; dynamic height 971.050 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	9.35	34.84	0	9.35	34.84	26.95
22	9.40	34.87	25	9.40	34.87	26.97
45	9.51	34.87	50	9.60	34.88	26.94
67	9.71	34.94	75	9.90	34.99	26.98
90	10.28	35.08	100	10.35	35.10	26.99
135	10.35	-------	150	10.05	35.05	27.00
179	8.72	34.79	200	9.05	34.93	27.07
269	8.32	35.03	300	7.10	34.92	27.36
225	9.39	35.12	400	5.60	34.90	27.54
335	5.83	34.79	600	4.40	34.98	27.74
443	5.39	34.95	800	3.90	34.97	27.80
624	4.29	34.98	1,000	3.75	34.96	27.80
1,227	3.62	34.95				

Station 2315; Apr. 10; latitude 44°38′ N., longitude 46°55′ W.; depth 4,024 meters; dynamic height 971.094 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	10.84	35.15	0	10.84	35.16	26.95
24	10.83	35 16	25	10.85	35.16	26.95
48	10.83	35.16	50	10.85	35.16	26.95
73	10.81	35.15	75	10.85	35.16	26.95
97	10.81	35.16	100	10.80	35.16	26.96
145	10.82	35.16	150	10.80	35.16	26.96
193	10.81	35.25	200	10.80	35.25	27.03
290	8.25	35.005	300	8.10	35.00	27.28
323	7.75	34.99	400	6.50	34.98	27.49
488	5.63	34.98	600	5.10	35.02	27.70
657	4.86	35.03	800	4.30	34.98	27.75
837	4.16	34.98	1,000	3.85	34.97	27.80
1,376	3.44	34.94				

Station 2316; Apr. 27; latitude 46°58′ N., longitude 48°41′ W.; depth 93 meters; dynamic height 971.003 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	−0.27	33.07	0	−0.27	33.07	26.58
15	−.28	33.07	25	−.40	33.07	26.59
40	−.55	33.12	50	−.55	33.18	26.68
86	−.39	33.49	75	−.45	33.40	26.86

Station 2317; Apr. 27; latitude 46°57′ N., longitude 48°09′ W.; depth 128 meters; dynamic height 971.008 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	−0.50	33.04	0	−0.50	33.04	26.57
27	−.48	33.04	25	−.50	33.04	26.57
54	−1.03	33.12	50	−.95	33.10	26.63
82	−1.46	33.33	75	−1.40	33.26	26.77
109	−.42	33.58	100	−.85	33.50	26.95

Station 2318; Apr. 27; latitude 46°56′ N., long. 47°45′ W.; depth 165 meters; dynamic height 971.003 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	−0.57	33.06	0	−0.57	33.06	26.58
26	−.55	33.06	25	−.55	33.06	26.58
52	−1.20	33.14	50	−1.10	33.13	26.66
77	−1.58	33.41	75	−1.55	33.40	26.90
103	−1.50	33.48	100	−1.55	33.47	26.96
155	−.33	33.71	150	−.45	33.68	27.08

Station 2319; Apr. 28; latitude 46°55′ N., longitude 47°09′ W.; depth 622 meters; dynamic height 970.926 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	−0.76	33.35	0	−0.76	33.35	26.82
24	−.75	33.35	25	−.75	33.35	26.82
48	−.81	33.62	50	−.80	33.64	27.06
72	−.26	33.70	75	−.20	33.70	27.09
96	−.02	33.74	100	.15	33.76	27.12
144	1.22	34.16	150	1.35	34.21	27.41
192	2.06	34.39	200	2.10	34.41	27.51
288	2.26	34.54	300	2.40	34.58	27.62
339	2.75	34.70	400	3.00	34.76	27.72
529	3.28	34.84	(600)	3.40	34.87	27.77

Station 2320; Apr. 28; latitude 46°55′ N., longitude 47°06′ W.; depth 1,097 meters; dynamic height 970.876 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	1.18	33.90	0	1.18	33.90	27.17
23	1.22	33.91	25	1.20	33.91	27.18
47	1.13	33.93	50	1.15	33.94	27.20
70	1.20	34.04	75	1.20	34.06	27.30
93	1.27	34.14	100	1.30	34.16	27.37
140	1.87	34.36	150	2.20	34.42	27.52
186	3.01	34.65	200	3.20	34.70	27.65
279	3.43	34.81	300	3.25	34.80	27.72
312	3.18	34.79	400	3.25	34.81	27.73
487	3.38	34.84	600	3.55	34.88	27.75
670	3.60	34.90	800	3.60	34.91	27.78
863	3.56	34.91	(1,000)	3.50	34.91	27.79

Station 2321; Apr. 28; latitude 46°56′ N., longitude 46°39′ W.; depth 631 meters; dynamic height 970.860 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	3.86	34.38	0	3.86	34.38	27.33
25	3.83	34.37	25	3.83	34.37	27.33
51	3.97	34.40	50	3.95	34.40	27.34
76	4.00	34.43	75	4.00	34.43	27.35
102	3.91	34.51	100	3.95	34.50	27.41
153	3.40	34.60	150	3.40	34.59	27.54
204	3.72	34.73	200	3.70	34.72	27.62
306	3.39	34.79	300	3.40	34.79	27.70
388	3.65	34.86	400	3.65	34.87	27.74
588	3.62	34.915	600	3.65	34.92	27.78

Station 2322; Apr. 28; latitude 46°56′ N., longitude 46°21′ W.; depth 311 meters; dynamic height 970.861 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	3.81	34.35	0	3.81	34.35	27.31
24	3.80	34.35	25	3.80	34.35	27.31
47	3.91	34.40	50	3.95	34.41	27.35
71	3.95	34.42	75	3.95	34.42	27.35
95	3.89	34.43	100	3.90	34.44	27.37
142	4.07	34.55	150	4.05	34.57	27.46
189	3.72	34.67	200	3.75	34.70	27.59
284	3.95	34.89	300	3.95	34.92	27.75

Station 2323; Apr. 28; latitude 46°58′ N., longitude 45°26′ W.; depth 220 meters; dynamic height 970.849 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	3.71	34.42	0	3.71	34.42	27.38
25	3.68	34.41	25	3.68	34.41	27.37
49	3.66	34.42	50	3.65	34.42	27.38
74	3.53	34.44	75	3.55	34.44	27.40
98	3.26	34.48	100	3.25	34.49	27.47
147	3.43	34.62	150	3.45	34.63	27.56
196	3.74	34.72	200	3.75	34.73	27.61

TABLE OF OCEANOGRAPHIC DATA—Continued

STATIONS OCCUPIED IN 1937—Continued

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
Station 2324; Apr. 28; latitude 47°00′ N., longitude 45°10′ W.; depth 165 meters; dynamic height 970.848 meters						
0	3.78	34.46	0	3.78	34.46	27.40
25	3.77	34.46	25	3.77	34.46	27.40
51	3.74	34.46	50	3.75	34.46	27.40
76	3.73	34.46	75	3.75	34.46	27.40
101	3.27	34.46	100	3.25	34.46	27.45
152	3.50	34.62	150	3.45	34.61	27.55
Station 2325; Apr. 28–29; latitude 47°01′ N., longitude 44°39′ W.; depth 125 meters; dynamic height 970.848 meters						
0	3.81	34.43	0	3.81	34.43	27.37
26	3.81	34.42	25	3.80	34.42	27.37
52	3.77	34.44	50	3.80	34.44	27.38
79	3.57	34.48	75	3.60	34.48	27.43
105	3.52	34.49	100	3.55	34.49	27.44
Station 2326; Apr. 29; latitude 46°54′ N., longitude 44°41′ W.; depth 165 meters; dynamic height 970.850 meters						
0	3.73	34.40	0	3.73	34.40	27.35
26	3.73	34.41	25	3.75	34.41	27.36
51	3.72	34.41	50	3.70	34.41	27.37
77	3.72	34.41	75	3.70	34.41	27.37
128	3.52	34.50	100	3.60	34.44	27.40
			(150)	3.50	34.56	27.51
Station 2327; Apr. 29; latitude 46°48′ N., longitude 44°41′ W.; depth 220 meters; dynamic height 970.856 meters						
0	3.61	34.38	0	3.61	34.38	27.35
26	3.60	34.38	25	3.60	34.38	27.35
51	3.60	34.38	50	3.60	34.38	27.35
77	3.58	34.38	75	3.60	34.38	27.35
129	3.45	34.44	100	3.50	34.39	27.37
180	3.50	34.56	150	3.45	34.49	27.45
			200	3.50	34.62	27.56
Station 2328; Apr. 29; latitude 46°37′ N., longitude 44°40′ W.; depth 640 meters; dynamic height 970.833 meters						
0	3.57	34.37	0	3.57	34.37	27.35
25	3.56	34.37	25	3.56	34.37	27.35
51	3.44	34.40	50	3.45	34.40	27.38
76	3.41	34.50	75	3.40	34.50	27.47
102	3.48	34.60	100	3.45	34.59	27.53
153	3.42	34.68	150	3.45	34.67	27.60
203	3.55	34.77	200	3.55	34.76	27.66
305	3.85	34.90	300	3.85	34.89	27.73
397	3.81	34.92	400	3.80	34.92	27.77
599	3.52	34.92	600	3.55	34.92	27.79

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
Station 2329; Apr. 29; latitude 46°26′ N., longitude 44°44′ W.; depth 1,866 meters; dynamic height 970.812 meters						
0	3.86	34.49	0	3.86	34.49	27.41
25	3.85	34.49	25	3.85	34.49	27.41
51	4.04	34.63	50	4.05	34.63	27.50
76	3.93	34.65	75	3.95	34.65	27.53
101	3.68	34.70	100	3.70	34.70	27.60
152	3.36	34.80	150	3.35	34.80	27.71
203	3.34	34.81	200	3.35	34.81	27.72
304	3.31	34.85	300	3.30	34.85	27.76
381	3.48	34.90	400	3.50	34.90	27.78
574	3.53	34.91	600	3.55	34.91	27.78
769	3.46	34.92	800	3.45	34.92	27.80
953	3.38	34.93	1,000	3.35	34.93	27.81
1,467	3.31	34.94				
Station 2330; Apr. 29; latitude 46°02′ N., longitude 44°48′ W.; depth 3,878 meters; dynamic height 970.832 meters						
0	5.00	34.61	0	5.00	34.61	27.39
22	4.89	34.61	25	4.90	34.61	27.40
44	4.86	34.61	50	4.90	34.61	27.40
66	4.95	34.63	75	4.90	34.64	27.42
88	4.75	34.65	100	4.30	34.64	27.49
132	3.69	34.63	150	3.60	34.66	27.58
177	3.51	34.73	200	3.50	34.78	27.68
265	3.45	34.85	300	3.45	34.86	27.75
230	3.44	34.82	400	3.50	34.87	27.76
347	3.45	34.86	600	3.55	34.92	27.79
466	3.52	34.90	800	3.45	34.93	27.80
598	3.53	34.92	1,000	3.35	34.94	27.82
998	3.36	34.94				
Station 2331; Apr. 29; latitude 46°06′ N., longitude 45°25′ W.; depth 2,652 meters; dynamic height 970.812 meters						
0	5.46	34.66	0	5.46	34.66	27.37
25	5.00	34.64	25	5.00	34.64	27.41
50	4.52	34.60	50	4.52	34.60	27.43
74	4.35	34.71	75	4.35	34.71	27.54
99	3.84	34.76	100	3.85	34.76	27.63
149	3.99	34.86	150	4.00	34.86	27.70
198	4.09	34.92	200	4.10	34.92	27.74
297	3.46	34.88	300	3.45	34.88	27.76
390	3.47	34.90	400	3.45	34.90	27.78
587	3.46	34.90	600	3.45	34.90	27.78
786	3.44	34.92	800	3.45	34.92	27.80
972	3.40	34.93	1,000	3.40	34.93	27.81
1,484	3.22	34.94				
Station 2332; Apr. 29; latitude 46°10′ N., longitude 46°01′ W.; depth 1,472 meters; dynamic height 970.840 meters						
0	2.90	33.82	0	2.90	33.82	26.98
25	1.86	34.10	25	1.86	34.10	27.28
51	3.82	34.46	50	3.80	34.45	27.39
76	3.55	34.52	75	3.55	34.52	27.47
102	3.83	34.66	100	3.80	34.66	27.56
153	3.92	34.75	150	3.90	34.75	27.62
204	3.90	34.83	200	3.90	34.82	27.68
306	4.06	34.92	300	4.05	34.92	27.74
406	3.52	34.88	400	3.55	34.88	27.75
610	3.65	34.93	600	3.65	34.92	27.78
800	3.54	34.94	800	3.55	34.94	27.80
1,016	3.48	34.94	1,000	3.50	34.94	27.81
1,319	3.35	34.93				

TABLE OF OCEANOGRAPHIC DATA—Continued

STATIONS OCCUPIED IN 1937—Continued

Station 2333; Apr. 29–30; latitude 46°14′ N., longitude 46°38′ W.; depth 1,033 meters; dynamic height 970.853 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	1.69	33.88	0	1.69	33.88	27.11
25	1.63	33.90	25	1.63	33.90	27.13
49	1.99	33.98	50	2.00	33.98	27.17
74	2.66	34.11	75	2.65	34.12	27.24
98	2.10	34.34	100	2.10	34.36	27.47
147	2.71	34.62	150	2.75	34.64	27.64
196	3.51	34.81	200	3.60	34.82	27.71
294	4.12	34.93	300	4.15	34.94	27.74
373	4.21	34.98	400	4.20	34.98	27.77
564	3.80	34.94	600	3.75	34.94	27.78
758	3.59	34.93	800	3.60	34.93	27.79
960	3.49	34.94	1,000	3.45	34.94	27.81

Station 2334; Apr. 30; latitude 46°16′ N., longitude 46°57′ W.; depth 1,097 meters; dynamic height 970.840 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	2.05	33.92	0	2.05	33.92	27.13
21	2.06	33.94	25	2.15	33.97	27.16
42	2.74	34.16	50	2.80	34.19	27.28
63	2.80	34.24	75	2.50	34.29	27.38
84	2.03	34.34	100	2.35	34.45	27.52
126	2.87	34.64	150	3.05	34.72	27.68
167	3.16	34.76	200	3.35	34.80	27.71
251	3.52	34.84	300	3.50	34.86	27.75
278	3.52	34.86	400	3.45	34.88	27.76
426	3.43	34.88	600	3.45	34.90	27.78
582	3.43	34.90	800	3.55	34.94	27.80
772	3.55	34.94	1,000	3.55	34.94	27.80

Station 2335; Apr. 30; latitude 46°18′ N., longitude 47°17′ W.; depth 622 meters; dynamic height 970.914 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	−0.39	33.19	0	−0.39	33.19	26.69
26	−.76	33.26	25	−.75	33.26	26.75
51	−1.18	33.52	50	−1.15	33.51	26.98
77	−.51	33.72	75	−.55	33.71	27.11
102	.72	33.96	100	.60	33.93	27.22
153	1.62	34.31	150	1.60	34.29	27.45
205	2.13	34.51	200	2.10	34.49	27.57
307	2.80	34.70	300	2.75	34.69	27.68
402	3.19	34.82	400	3.20	34.82	27.75
604	3.43	34.88	600	3.45	34.88	27.76

Station 2336; Apr. 30; latitude 46°21′ N., longitude 47°44′ W.; depth 165 meters, dynamic height 971.017 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
3	−0.27	33.05	0	−0.25	33.05	26.56
29	−.32	33.06	25	−.30	33.06	26.57
55	−1.35	33.22	50	−1.15	33.18	26.70
81	−1.57	33.44	75	−1.55	33.38	26.88
106	−.93	33.60	100	−1.10	33.57	27.02
158	−.10	33.76	150	−.20	33.75	27.13

Station 2337; Apr. 30; latitude 46°23′ N., longitude 48°00′ W.; depth 126 meters, dynamic height 971.017 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	−0.11	33.06	0	−0.11	33.06	26.56
26	−.31	33.09	25	−.30	33.09	26.59
53	−.78	33.17	50	−.65	33.16	26.67
79	−1.36	33.43	75	−1.30	33.37	26.86
106	−1.13	33.58	100	−1.20	33.56	27.02

Station 2338; Apr. 30; latitude 46°27′ N., longitude 48°32′ W.; depth 88 meters; dynamic height 971.017 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	0.33	33.06	0	0.33	33.06	26.54
27	.33	33.07	25	.35	33.07	26.55
53	−.02	33.12	50	0.00	33.11	26.60
80	−.21	33.68	75	−.20	33.53	26.95

Station 2339; Apr. 30; latitude 46°30′ N., longitude 49°00′ W.; depth 70 meters; dynamic height 971.005 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	0.70	33.15	0	0.70	33.15	26.60
28	.68	33.15	25	.70	33.15	26.60
56	−0.06	33.28	50	.10	33.24	26.71

Station 2340; Apr. 30; latitude 46°16′ N., longitude 48°40′ W.; depth 88 meters; dynamic height 971.002 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	0.46	-------	0	0.46	33.09	26.56
26	.45	33.09	25	.45	33.09	26.56
52	.26	33.22	50	.25	33.19	26.66
78	−.10	33.70	75	−.05	33.64	27.03

Station 2341; Apr. 30; latitude 46°02′ N., longitude 48°20′ W.; depth 113 meters; dynamic height 971.003 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	−0.22	33.11	0	−0.22	33.11	26.61
21	−.25	33.11	25	−.30	33.11	26.61
47	−1.09	33.23	50	−1.20	33.24	26.75
73	−1.48	33.41	75	−1.50	33.42	26.92
99	−.61	33.62	100	−.50	33.64	27.05

Station 2342; May 1; latitude 45°51′ N., longitude 48°04′ W.; depth 165 meters; dynamic height 971.002 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	−0.37	33.07	0	−0.37	33.07	26.58
26	−.38	33.10	25	−.40	33.10	26.61
52	−.69	33.35	50	−.60	33.33	26.80
79	−1.49	33.47	75	−1.50	33.46	26.95
105	−1.23	33.55	100	−1.35	33.53	26.99
157	−.39	33.71	150	−.50	33.69	27.09

Station 2343; May 1; latitude 45°45′ N., longitude 47°56′ W.; depth 631 meters; dynamic height 970.950 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	−0.14	33.32	0	−0.14	33.32	26.78
24	−.10	33.34	25	−.10	33.34	26.79
48	−.41	33.48	50	−.45	33.49	26.93
72	−1.08	33.54	75	−1.05	33.55	27.00
96	−.72	33.66	100	−.65	33.69	27.10
144	.41	33.94	150	.60	33.97	27.26
192	1.67	34.29	200	1.75	34.32	27.47
288	2.28	34.54	300	2.30	34.56	27.62
312	2.35	34.57	400	2.70	34.69	27.68
486	3.01	34.77	(600)	3.40	34.85	27.75

TABLE OF OCEANOGRAPHIC DATA—Continued

STATIONS OCCUPIED IN 1937—Continued

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
Station 2344; May 1; latitude 45°43′ N., longitude 47°53′ W.; depth 1,097 meters; dynamic height 970.924 meters						
0	−0.30	33.40	0	−0.30	33.40	26.85
24	−.10	33.42	25	−.10	33.42	26.86
49	−1.29	33.54	50	−1.30	33.55	27.01
73	−.59	33.66	75	−.55	33.67	27.08
97	−.33	33.76	100	−.30	33.78	27.15
146	1.25	34.11	150	1.35	34.14	27.35
195	1.97	34.44	200	2.00	34.45	27.55
292	2.55	34.66	300	2.60	34.67	27.68
344	2.89	34.72	400	3.10	34.77	27.72
521	3.31	34.84	600	3.45	34.86	27.75
700	3.50	34.88	800	3.55	34.91	27.78
896	3.57	34.93	1,000	3.55	34.93	27.79
Station 2345; May 1; latitude 45°34′ N., longitude 47°46′ W.; depth 1,509 meters; dynamic height 970.893 meters						
0	0.79	33.71	0	0.79	33.71	27.04
25	.79	33.71	25	.79	33.71	27.04
51	96	33.80	50	.95	33.80	27.10
76	.62	33.91	75	.60	33.91	27.21
102	.60	34.01	100	.60	34.00	27.28
153	1.96	34.35	150	1.85	34.33	27.46
203	3.26	34.64	200	3.20	34.61	27.58
305	3.97	34.86	300	3.95	34.85	27.69
399	3.46	34.85	400	3.45	34.85	27.74
600	3.49	34.90	600	3.50	34.90	27.78
802	3.69	34.935	800	3.70	34.93	27.78
989	3.62	34.945	1,000	3.60	34.94	27.80
Station 2346; May 1; latitude 45°18′ N.; longitude 47°34′ W.; depth 2,616 meters; dynamic height 970.898 meters						
0	5.14	34.14	0	5.14	34.14	27.00
25	5.32	34.21	25	5.32	34.21	27.04
49	5.64	34.26	50	5.65	34.26	27.03
74	4.94	34.34	75	4.90	34.34	27.18
99	4.71	34.41	100	4.70	34.41	27.26
148	5.50	34.71	150	5.50	34.71	27.41
197	4.21	34.70	200	4.25	34.70	27.54
296	4.63	34.94	300	4.65	34.95	27.70
344	4.60	34.98	400	4.40	34.94	27.74
518	3.98	34.96	600	3.90	34.96	27.79
693	3.89	34.965	800	3.80	34.97	27.81
868	3.72	34.975	1,000	3.65	34.96	27.81
1,351	3.32	34.945				
Station 2347; May 1; latitude 45°18′ N., longitude 46°51′ W.; depth 2,981 meters; dynamic height 970.896 meters						
0	6.36	34.36	0	6.36	34.36	27.02
25	6.09	34.34	25	6.09	34.34	27.04
50	5.72	34.30	50	5.72	34.30	27.06
76	4.86	34.36	75	4.90	34.36	27.20
101	4.74	34.43	100	4.75	34.43	27.27
151	5.04	34.70	150	5.05	34.69	27.44
202	5.10	34.86	200	5.10	34.85	27.56
303	4.11	34.88	300	4.15	34.88	27.69
367	3.48	34.84	400	3.50	34.84	27.73
550	3.52	34.90	600	3.55	34.91	27.78
731	3.59	34.93	800	3.60	34.94	27.80
933	3.54	34.94	1,000	3.50	34.94	27.81
1,311	3.38	34.94				
Station 2348; May 1; latitude 45°19′ N., longitude 46°14′ W.; depth 3,420 meters; dynamic height 970.839 meters						
0	5.04	34.59	0	5.04	34.59	27.36
25	4.99	34.59	25	4.99	34.59	27.37
50	4.94	34.60	50	4.94	34.60	27.38
75	4.25	34.58	75	4.25	34.58	27.44
100	4.29	34.66	100	4.29	34.66	27.51
150	4.00	34.72	150	4.00	34.72	27.59
199	3.83	34.79	200	3.85	34.79	27.65
299	3.57	34.86	300	3.55	34.86	27.74
353	3.54	34.89	400	3.55	34.90	27.77
535	3.61	34.92	600	3.65	34.92	27.78
723	3.60	34.93	800	3.60	34.93	27.79
924	3.52	34.935	1,000	3.50	34.94	27.81
1,296	3.55	34.945				
Station 2349; May 2; latitude 44°51′ N., longitude 46°24′ W.; depth 3,612 meters; dynamic height 970.931 meters						
0	4.33	33.91	0	4.33	33.73	26.76
25	3.28	33.60	25	3.28	33.60	26.76
50	3.63	33.90	50	3.63	33.90	26.96
75	4.54	34.19	75	4.54	34.19	27.10
100	5.03	34.34	100	5.03	34.34	27.17
150	4.97	34 55	150	4.97	34.55	27.34
200	4.29	-------	200	4.29	34.64	27.49
300	4.49	34.87	300	4.49	34.87	27.65
382	4.23	34.92	400	4.20	34.93	27.73
576	4.15	34.99	600	4.15	34.99	27.78
771	3.89	34.98	800	3.90	34.98	27.80
1,080	3.55	34.96	1,000	3.65	34.96	27.81
1,466	3.39	34.96				
Station 2350; May 2; latitude 44°24′ N., longitude 46°34′ W.; depth 3,896 meters; dynamic height 971.146 meters						
0	11.92	35.20	0	11.92	35.20	26.78
25	11.33	35.20	25	11.33	35.20	26.89
51	11.03	35.20	50	11.05	35.20	26.94
76	10.84	35.22	75	10.85	35.22	26.99
102	10.95	35.26	100	10.95	35.25	27.00
153	11.03	35.29	150	11.05	35.29	27.00
204	11.01	35.29	200	11.05	35.29	27.00
306	8.58	34.93	300	8.70	34.94	27.14
400	7.94	35.02	400	7.95	35.02	27.32
602	5.44	35.01	600	5.50	35.01	27.64
806	4.38	35.00	800	4.40	35.00	27.76
1,022	3.93	34.99	1,000	3.95	34.99	27.80
1,412	3.50	34.96				
Station 2351; May 2; latitude 44°32′ N., longitude 47°07′ W.; depth 3,850 meters; dynamic height 971.065 meters						
0	11.59	35.05	0	11.59	35.05	26.72
25	11.59	35.05	25	11.59	35.05	26.72
50	11.60	35.04	50	11.60	35.04	26.72
75	11.60	35.05	75	11.60	35.05	26.72
100	11.47	35.30	100	11.47	35.30	26.95
150	10.82	35.28	150	10.82	35.28	27.04
200	9.57	35.16	200	9.57	35.16	27.16
300	6.88	34.91	300	6.88	34.91	27.38
409	5.95	35.00	400	6.00	34.99	27.56
612	4.24	34.94	600	4.30	34.94	27.72
814	4.15	35.00	800	4.15	35.00	27.79
1,032	3.77	34.97	1,000	3.80	34.97	27.81
1,421	3.42	34.94				

TABLE OF OCEANOGRAPHIC DATA—Continued

STATIONS OCCUPIED IN 1937—Continued

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
Station 2352; May 2; latitude 44°40′ N., longitude 47°40′ W ; depth 3,685 meters, dynamic height 970.940 meters						
0	6.05	33.80	0	6.05	33.80	26.62
25	4.89	33.74	25	4.89	33.74	26.71
51	4.41	33.74	50	4.45	33.74	26.76
76	2.84	33.91	75	2.85	33.91	27.05
102	3.39	34.14	100	3.25	34.11	27.17
153	5.09	34.66	150	5.05	34.65	27.41
204	4.52	34.68	200	4.55	34.67	27.49
306	4.38	34.86	300	4.40	34.85	27.64
406	4.65	34.97	400	4.65	34.97	27.72
608	4.28	35.00	600	4.30	35.00	27.77
811	3.81	34.975	800	3.85	34.98	27.80
1,027	3.60	34.96	1,000	3.60	34.96	27.82
1,417	3.38	34.96				
Station 2353; May 2; latitude 44°47′ N., longitude 48°13′ W.; depth 3,091 meters; dynamic height 970.891 meters						
0	4.60	33.71	0	4.60	33.71	26.72
25	4.02	33.66	25	4.02	33.66	26.75
51	3.39	33.92	50	3.40	33.91	27.00
76	2.59	34.03	75	2.65	34.03	27.16
102	1.32	34.10	100	1.35	34.09	27.31
153	3.82	34.63	150	3.70	34.60	27.52
204	5.18	34.91	200	5.15	34.90	27.60
306	4.04	34.89	300	4.05	34.89	27.71
397	4.42	35.00	400	4.40	35.00	27.76
595	3.99	34.98	600	4.00	34.98	27.79
793	3.74	34.98	800	3.75	34.98	27.81
1,006	3.60	34.97	1,000	3.60	34.97	27.83
1,392	3.36	34.96				
Station 2354; May 2; latitude 44°54′ N., longitude 48°44′ W.; depth 1,454 meters; dynamic height 970.878 meters						
0	2.95	33.80	0	2.95	33.80	26.95
26	4.27	34.07	25	4.25	34.07	27.05
51	4.52	34.16	50	4.50	34.16	27.09
77	3.39	34.15	75	3.40	34.15	27.19
102	3.53	34.37	100	3.50	34.35	27.34
153	3.99	34.66	150	3.95	34.65	27.53
205	4.08	34.77	200	4.10	34.77	27.62
307	3.59	34.93	300	3.60	34.82	27.71
384	4.21	34.96	400	4.20	34.96	27.76
577	3.60	34.92	600	3.60	34.92	27.79
772	3.60	34.93	800	3.60	34.93	27.79
986	3.60	34.955	1,000	3.60	34.96	27.82
Station 2355; May 3; latitude 44°58′ N.; longitude 49°01′ W.; depth 622 meters; dynamic height 970.999 meters						
0	−0.04	33.12	0	−0.04	33.12	26.61
25	−.84	33.20	25	−.84	33.20	26.71
49	−1.55	33.40	50	−1.55	33.41	26.91
74	−1.56	33.47	75	−1.55	33.48	26.96
98	−.89	33.64	100	−.85	33.66	27.08
147	−.01	33.83	150	.05	33.84	27.19
196	.34	33.94	200	.40	33.95	27.26
294	1.30	34.21	300	1.40	34.24	27.43
328	*1.83	34.37	400	2.55	34.59	27.62
492	3.01	34.76	(600)	3.40	34.86	27.76
Station 2356; May 3; latitude 45°00′ N., longitude 49°05′ W.; depth 220 meters; dynamic height 971.033 meters						
0	−0.02	33.12	0	−0.02	33.12	26.61
25	−.93	33.22	25	−.93	33.32	26.73
51	−1.06	33.48	50	−1.05	33.48	26.94
76	−1.01	33.51	75	−1.00	33.51	26.97
126	−.81	33.60	100	−.90	33.55	27.00
177	−.78	33.60	150	−.75	33.60	27.03
			(200)	−.75	33.60	27.03
Station 2357; May 3; latitude 45°01′ N., longitude 49°09′ W.; depth 88 meters; dynamic height 971.047 meters						
0	−0.04	33.12	0	−0.04	33.12	26.61
26	−.04	33.12	25	−.05	33.12	26.61
52	−.21	33.18	50	−.20	33.17	26.66
78	−.77	33.39	75	−.70	33.38	26.85
Station 2358; May 3; latitude 45°07′ N., longitude 49°34′ W.; depth 60 meters; dynamic height 971.044 meters						
0	0.84	33.24	0	0.84	33.24	26.67
26	.74	33.26	25	.75	33.26	26.68
46	.56	33.28	50	.50	33.29	26.71
Station 2359; May 3; latitude 44°11′ N., longitude 49°42′ W.; depth 49 meters; dynamic height 971.121 meters						
0	1.16	33.20	0	1.16	33.20	26.62
18	1.05	33.20	25	1.05	33.20	26.63
39	1.03	33.21	(50)	1.05	33.22	26.64
Station 2360; May 3; latitude 44°04′ N., longitude 49°12′ W.; depth 95 meters; dynamic height 971.120 meters						
0	0.32	33.18	0	0.32	33.18	26.64
26	.25	33.20	25	.25	33.20	26.67
53	.16	33.18	50	.20	33.18	26.65
79	.03	33.20	75	.05	33.19	26.67
Station 2361; May 3; latitude 44°00′ N., longitude 48°55′ W.; depth 659 meters; dynamic height 971.029 meters						
0	0.04	33.18	0	0.04	33.18	26.66
25	−.53	33.30	25	−.53	33.30	26.77
50	−.90	33.52	50	−.90	33.52	26.98
75	−.84	33.56	75	−.84	33.56	27.00
100	−.80	33.58	100	−.80	33.58	27.01
150	−.60	33.64	150	−.60	33.64	27.05
200	−.01	33.82	200	−.01	33.82	27.18
300	1.17	34.15	300	1.17	34.15	27.37
328	*1.40	34.23	400	2.00	34.44	27.54
515	2.94	34.72	(600)	3.30	34.83	27.74

TABLE OF OCEANOGRAPHIC DATA—Continued

STATIONS OCCUPIED IN 1937—Continued

Station 2362; May 3; latitude 43°58′ N., longitude 48°47′ W.; depth 1,481 meters; dynamic height 970.941 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σt
0	−0.02	33.23	0	−0.02	33.23	26.70
24	.60	33.51	25	.60	33.52	26.90
48	−.75	33.64	50	−.70	33.65	27.07
73	−.19	33.76	75	−.15	33.77	27.15
97	.53	33.88	100	.60	33.90	27.20
146	1.05	34.13	150	1.10	34.14	27.37
194	1.36	34.22	200	1.40	34.23	27.42
291	2.28	34.52	300	2.30	34.54	27.60
291	2.24	34.53	400	2.95	34.71	27.68
437	3.06	34.75	600	3.45	34.86	27.75
584	3.45	34.86	800	3.60	34.91	27.78
755	3.57	34.90	(1,000)	3.60	34.93	27.79
1,089	3.58	--------				

Station 2363; May 4; latitude 43°54′ N., longitude 48°20′ W.; depth 3,228 meters; dynamic height 970.960 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σt
0	6.14	33.74	0	6.15	33.74	26.56
25	5.68	33.70	25	5.68	33.70	26.58
51	6.63	34.05	50	6.65	34.05	26.74
76	4.56	34.08	75	4.55	34.08	27.01
102	4.66	34.26	100	4.60	34.24	27.14
153	5.80	34.57	150	5.75	34.55	27.25
204	5.54	34.78	200	5.55	34.77	27.45
306	5.39	34.98	300	5.40	34.97	27.63
406	4.89	35.02	400	4.90	35.02	27.73
611	3.95	34.95	600	4.00	34.95	27.77
816	3.82	34.96	800	3.85	34.96	27.79
1,028	3.68	34.97	1,000	3.70	34.97	27.82
1,407	3.37	34.94				

Station 2364; May 4; latitude 43°49′ N., longitude 47°46′ W.; depth 3,887 meters; dynamic height 971.088 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σt
0	9.46	34.41	0	9.46	34.41	26.60
25	12.32	35.18	25	12.32	35.18	26.68
51	12.40	35.21	50	12.40	35.21	26.70
76	13.27	35.50	75	13.30	35.50	26.74
102	13.04	35.54	100	13.10	35.54	26.81
153	10.60	35.15	150	10.70	35.17	26.98
204	9.84	35.20	200	9.90	35.20	27.14
306	8.02	35.08	300	8.15	35.08	27.33
404	6.24	35.02	400	6.30	35.02	27.55
604	4.65	34.98	600	4.70	34.98	27.71
802	3.87	34.95	800	3.85	34.95	27.78
1,017	3.76	34.96	1,000	3.80	34.96	27.80
1,405	3.52	34.95				

Station 2365; May 4; latitude 43°43′ N., longitude 47°15′ W.; depth 3,987 meters, dynamic height 970.993 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σt
0	8.37	34.22	0	8.37	34.22	26.63
25	8.03	34.24	25	8.04	34.24	26.69
51	8.08	34.33	50	8.10	34.33	26.75
76	7.23	34.29	75	7.30	34.29	26.84
102	5.70	34.25	100	5.80	34.25	27.01
153	6.64	34.71	150	6.65	34.71	27.26
204	5.75	34.73	200	5.80	34.73	27.38
306	5.08	34.83	300	5.10	34.82	27.54
401	5.27	35.00	400	5.25	35.00	27.67
599	4.66	35.03	600	4.65	35.03	27.76
797	3.88	34.96	800	3.90	34.96	27.79
1,010	3.82	34.98	1,000	3.85	34.98	27.80
1,399	3.49	34.96				

Station 2366; May 4; latitude 43°35′ N., longitude 46°26′ W.; depth 4,372 meters; dynamic height 971.088 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σt
0	11.56	34.78	0	11.56	34.78	26.52
26	11.29	34.84	25	11.30	34.84	26.62
51	11.43	34.92	50	11.45	34.91	26.65
77	12.89	35.32	75	12.90	35.32	26.68
102	11.38	35.08	100	11.50	35.09	26.77
153	10.54	35.13	150	10.60	35.12	26.96
205	10.09	35.22	200	10.15	35.21	27.11
307	6.71	34.86	300	6.80	34.87	27.37
389	6.09	34.96	400	6.00	34.97	27.55
585	4.76	35.01	600	4.70	35.01	27.74
782	4.12	34.975	800	4.10	34.98	27.78
991	3.99	35.00	1,000	4.00	35.00	27.81
1,368	3.57	34.97				

Station 2367; May 4; latitude 43°11′ N.; longitude 46°41′ W.; depth 3,923 meters; dynamic height 970.911 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σt
0	7.90	34.03	0	7.90	34.03	26.54
25	6.67	34.05	25	6.67	34.05	26.73
49	5.72	34.13	50	5.70	34.13	26.92
74	4.04	34.12	75	4.00	34.12	27.11
98	3.77	34.31	100	3.75	34.33	27.30
147	3.71	34.55	150	3.75	34.56	27.48
197	4.37	34.76	200	4.40	34.77	27.58
295	4.99	34.97	300	5.00	34.97	27.68
387	4.59	34.98	400	4.55	34.98	27.73
572	4.40	35.02	600	4.35	35.02	27.79
751	4.03	35.01	800	3.95	35.00	27.81
959	3.72	34.975	1,000	3.70	34.98	27.82
1,340	3.41	34.955				

Station 2368; May 4–5; latitude 42°46′ N., longitude 46°57′ W.; depth 3,978 meters; dynamic height 971.106 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σt
0	10.72	34.55	0	10.72	34.55	26.50
23	10.41	34.56	25	10.40	34.56	26.56
46	10.06	34.59	50	10.15	34.62	26.65
68	10.78	34.80	75	11.15	34.89	26.68
91	11.61	35.05	100	11.70	35.11	26.75
137	11.87	35.28	150	11.80	35.32	26.90
182	11.18	35.36	200	10.25	35.27	27.14
279	5.16	34.56	300	5.45	34.62	27.34
243	7.39	34.84	400	5.45	34.85	27.52
359	6.06	34.88	600	4.50	34.94	27.70
472	4.46	34.81	800	4.00	34.95	27.77
614	4.51	34.95	(1,000)	3.65	34.94	27.79
892	3.78	34.94				

Station 2369; May 5; latitude 43°00′ N., longitude 47°39′ W.; depth 3,512 meters; dynamic height 970.987 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σt
0	8.78	34.11	0	8.78	34.11	26.47
25	9.02	34.29	25	9.02	34.29	26.57
50	9.51	34.68	50	9.52	34.68	26.80
76	8.95	34.80	75	8.95	34.80	26.99
101	9.30	35.01	100	9.30	35.01	27.10
151	7.91	34.98	150	7.95	34.98	27.28
201	6.81	34.90	200	6.85	34.90	27.38
302	5.08	34.83	300	5.15	34.83	27.54
398	4.26	34.84	400	4.25	34.84	27.65
598	4.12	34.97	600	4.15	34.97	27.77
797	3.96	34.975	800	3.95	34.97	27.79
1,009	3.72	34.965	1,000	3.75	34.97	27.81
1,398	3.42	34.945				

TABLE OF OCEANOGRAPHIC DATA—Continued

STATIONS OCCUPIED IN 1937—Continued

Station 2370; May 5; latitude 43°16′ N., longitude 48°23′ W.; depth 3,008 meters; dynamic height 970.915 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	5.37	33.64	0	5.37	33.64	26.57
25	4.26	33.61	25	4.26	33.61	26.68
50	4.29	33.83	50	4.29	33.83	26.84
75	3.65	34.04	75	3.65	34.04	27.08
100	3.21	34.17	100	3.21	34.17	27.23
150	3.27	34.50	150	3.27	34.50	27.48
201	3.94	34.73	200	3.95	34.73	27.59
301	4.32	34.90	300	4.30	34.90	27.69
406	4.12	34.94	400	4.15	34.94	27.74
608	3.80	34.955	600	3.85	34.95	27.78
810	3.66	34.95	800	3.70	34.95	27.80
1,027	3.53	34.95	1,000	3.55	34.95	27.81
1,417	3.34	34.945				

Station 2371; May 5; latitude 43°21′ N., longitude 49°07′ W.; depth 2,030 meters; dynamic height 970.905 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	0.91	33.32	0	0.91	33.32	26.72
26	.83	33.30	25	.85	33.30	26.71
51	−.11	33.44	50	−.10	33.43	26.86
77	.03	33.76	75	.05	33.75	27.12
103	1.11	34.03	100	1.00	34.00	27.26
154	2.26	34.45	150	2.15	34.41	27.51
205	4.34	34.82	200	4.30	34.80	27.62
308	4.10	34.88	300	4.10	34.87	27.70
395	4.05	34.93	400	4.05	34.94	27.75
592	4.14	34.99	600	4.15	34.99	27.78
788	3.84	34.97	800	3.85	34.97	27.80
1,000	3.65	34.96	1,000	3.65	34.96	27.81
1,387	3.40	34.95				

Station 2372; May 5; latitude 42°39′ N., longitude 49°15′ W.; depth 2,506 meters; dynamic height 970.903 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	5.91	33.68	0	5.91	33.68	26.54
25	4.52	33.64	25	4.52	33.64	26.67
51	2.86	33.86	50	2.95	33.85	26.99
76	2.36	34.14	75	2.35	34.15	27.28
102	5.48	34.69	100	5.40	34.68	27.39
153	4.96	34.70	150	4.95	34.70	27.46
204	5.55	34.90	200	5.55	34.89	27.54
306	5.03	34.98	300	5.05	34.98	27.67
405	4.65	35.01	400	4.65	35.01	27.75
607	4.35	35.03	600	4.35	35.03	27.80
809	3.99	35.01	800	4.00	35.01	27.82
1,023	3.60	34.97	1,000	3.65	34.97	27.82
1,412	3.36	34.96				

Station 2373; May 6; latitude 42°24′ N., longitude 48°33′ W.; depth 3,283 meters; dynamic height 970.928 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	6.64	33.81	0	6.64	33.81	26.55
24	4.41	33.80	25	4.40	33.80	26.81
49	3.19	33.79	50	3.20	33.79	26.92
73	2.72	33.97	75	2.70	33.99	27.12
97	2.98	34.14	100	3.00	34.17	27.25
146	3.98	34.52	150	4.05	34.54	27.43
195	5.17	34.80	200	5.15	34.81	27.53
292	4.26	34.84	300	4.20	34.84	27.66
345	4.00	34.85	400	4.00	34.88	27.71
521	4.09	34.96	600	3.95	34.95	27.77
700	3.74	34.945	800	3.70	34.94	27.79
899	3.66	34.94	1,000	3.65	34.94	27.79
1,275	3.47	34.95				

Station 2374; May 6; latitude 42°09′ N., longitude 47°52′ W.; depth 3,740 meters; dynamic height 971.145 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	16.45	36.10	0	16.45	36.10	26.50
25	16.44	36.10	25	16.45	36.10	26.50
49	15.35	35.86	50	15.30	35.84	26.56
74	13.93	35.56	75	13.95	35.56	26.65
99	13.86	35.60	100	13.85	35.60	26.70
148	13.48	35.64	150	13.45	35.64	26.81
197	12.84	35.64	200	12.80	35.62	26.95
296	9.19	35.20	300	9.15	35.20	27.27
272	9.36	35.20	400	7.25	35.09	27.47
402	7.14	35.08	600	4.50	34.95	27.71
528	4.31	34.83	800	4.45	35.02	27.78
685	4.76	35.03	1,000	3.80	34.98	27.81
990	3.80	34.985				

Station 2375; May 6; latitude 41°48′ N., longitude 47°13′ W.; depth 4,007 meters; dynamic height 971.265 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	15.47	35.74	0	15.47	35.74	26.46
25	15.78	35.90	25	15.78	35.90	26.50
50	14.52	35.59	50	14.52	35.59	26.54
74	15.24	35.83	75	15.24	35.83	26.57
99	13.85	35.50	100	13.85	35.50	26.62
149	13.21	35.40	150	13.20	35.40	26.68
198	12.83	35.44	200	12.80	35.44	26.79
297	12.26	35.56	300	12.20	35.56	27.00
353	11.07	35.46	400	9.80	35.35	27.28
532	6.87	35.03	600	6.10	35.03	27.58
711	5.28	35.05	800	4.90	35.05	27.75
911	4.53	35.035	1,000	4.35	35.02	27.79
1,288	3.84	34.995				

Station 2376; May 6; latitude 41°01′ N., longitude 47°27′ W.; depth 3,438 meters: dynamic height 971.159 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	14.16	35.52	0	14.16	35.52	26.58
25	13.87	35.48	25	13.87	35.48	26.60
51	13.83	35.48	50	13.85	35.48	26.61
76	12.88	35.32	75	12.90	35.32	26.68
102	12.66	35.30	100	12.70	35.30	26.71
153	12.43	35.30	150	12.45	35.30	26.75
204	12.34	35.44	200	12.35	35.44	26.88
306	9.12	35.08	300	9.55	35.10	27.12
367	4.77	34.59	400	4.50	34.63	27.45
536	4.14	34.83	600	4.20	34.90	27.71
694	4.29	34.965	800	4.20	34.99	27.78
888	4.10	35.00	1,000	3.95	35.00	27.81
1,253	3.73	34.985				

Station 2377; May 7; latitude 41°23′ N., longitude 48°18′ W.; depth 3,447 meters; dynamic height 971.153 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	14.05	35.50	0	14.05	35.50	26.88
25	13.77	35.50	25	13.77	35.50	26.63
50	13.07	35.37	50	13.07	35.37	26.68
74	12.71	35.31	75	12.70	35.31	26.72
99	12.79	35.34	100	12.80	35.34	26.72
149	12.07	35.30	150	12.10	35.30	26.82
199	12.85	35.65	200	12.85	35.65	26.94
298	10.06	35.30	300	9.95	35.29	27.20
343	8.69	35.13	400	7.35	35.05	27.43
520	5.46	34.96	600	4.50	34.92	27.69
699	3.68	34.86	800	3.95	34.94	27.76
874	4.18	35.00	1,000	4.05	34.99	27.79
1,174	3.65	34.97				

TABLE OF OCEANOGRAPHIC DATA—Continued

STATIONS OCCUPIED IN 1937—Continued

Station 2378; May 7; latitude 41°45′ N., longitude 49°17′W., depth 3,182 meters; dynamic height 971.140 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	13.58	35.35	0	13.58	35.35	26.56
25	13.60	35.37	25	13.60	35.37	26.58
50	13.58	35.44	50	13.58	35.44	26.63
75	12.69	35.27	75	12.69	35.27	26.69
100	11.93	35.17	100	11.93	35.17	26.76
150	12.55	35.45	150	12.55	35.45	26.85
201	12.24	35.54	200	12.25	35.54	26.98
301	9.52	35.24	300	9.60	35.25	27.23
375	6.49	34.86	400	6.30	34.88	27.44
560	5.31	35.04	600	5.10	35.04	27.71
745	4.49	35.02	800	4.35	35.02	27.79
944	4.07	35.01	1,000	4.00	35.01	27.82
1,321	3.73	34.98				

Station 2379; May 7; latitude 42°04′ N., longitude 50°04′ W.; depth 3,603 meters; dynamic height 970.980 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	4.68	33.52	0	4.68	33.52	26.56
24	2.83	33.50	25	2.80	33.50	26.73
48	2.59	33.54	50	2.55	33.54	26.78
73	1.12	33.53	75	1.10	33.53	26.87
97	—.48	33.60	100	—.40	33.63	27.04
146	1.84	33.97	150	1.80	34.00	27.21
194	1.61	34.14	200	1.65	34.17	27.36
291	3.27	34.62	300	3.55	34.67	27.59
317	3.96	34.74	400	4.55	34.91	27.68
477	4.65	34.98	600	4.60	35.03	27.76
638	4.55	35.03	800	4.20	35.01	27.80
822	4.13	35.005	1,000	3.90	35.00	27.82
1,183	3.77	34.995				

Station 2380; May 7; latitude 42°28′ N., longitude 49°50′ W.; depth 2,789 meters; dynamic height 970.916 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	3.47	33.50	0	3.47	33.50	26.66
25	2.99	33.58	25	2.99	33.58	26.77
51	2.01	33.60	50	2.05	33.60	26.88
76	1.29	33.84	75	1.30	33.85	27.12
101	1.17	34.09	100	1.15	34.08	27.31
152	4.47	34.63	150	4.25	34.61	27.47
203	5.11	34.85	200	5.10	34.85	27.56
304	4.85	34.94	300	4.85	34.95	27.67
394	4.63	34.99	400	4.60	34.99	27.73
592	4.27	35.005	600	4.25	35.00	27.78
791	3.93	34.995	800	3.95	34.99	27.80
1,001	3.60	34.96	1,000	3.60	34.96	27.82
1,391	3.42	34.955				

Station 2381; May 8; latitude 42°55′ N., longitude 49°49′ W.; depth 640 meters; dynamic height 970.993 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	0.87	33.23	0	0.87	33.23	26.65
25	—.87	33.41	25	—.87	33.41	26.88
51	—.99	33.50	50	—1.00	33.49	26.95
76	—.85	33.55	75	—.85	33.55	26.99
102	—.72	33.60	100	—.75	33.59	27.02
153	.08	33.84	150	0.00	33.83	27.18
204	.59	34.00	200	.55	33.98	27.27
306	3.25	34.62	300	3.15	34.60	27.57
407	3.33	34.79	400	3.35	34.79	27.70
604	3.43	34.81	600	3.45	34.81	27.71

Station 2382; May 8; latitude 43°08′ N., longitude 49°54′ W.; depth 88 meters; dynamic height 971.019 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	0.84	33.22	0	0.84	33.22	26.65
16	.41	33.27	25	.10	33.30	26.75
43	—.48	33.34	50	—.55	33.35	26.82
70	—.72	33.41	75	—.75	33.43	26.89

Station 2383; May 8; latitude 43°19′ N., longitude 50°10′ W.; depth 60 meters; dynamic height 971.034 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	1.89	33.14	0	1.89	33.14	26.52
28	1.12	33.19	25	1.20	33.19	26.61
50	.34	33.23	50	.34	33.23	26.68

Station 2384; May 8; latitude 43°08′ N., longitude 50°40′ W.; depth 89 meters; dynamic height 971.036 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	1.62	33.16	0	1.62	33.16	26.54
26	0.25	33.28	25	.25	33.28	26.73
51	—.17	33.32	50	—.15	33.32	26.78
77	—.48	33.42	75	—.45	33.41	26.87

Station 2385; May 8; latitude 43°00′ N., longitude 50°51′ W.; depth 686 meters; dynamic height 971.039 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	1.55	33.17	0	1.55	33.17	26.56
26	1.78	33.19	25	1.80	33.19	26.56
51	.42	33.28	50	.45	33.28	26.72
77	—.18	33.38	75	—.15	33.37	26.82
103	—.75	33.44	100	—.70	33.43	26.89
154	—.93	33.54	150	—.95	33.53	26.98
205	—.45	33.68	200	—.50	33.67	27.08
308	.70	34.01	300	.65	33.99	27.27
410	3.06	34.68	400	2.90	34.64	27.63
606	3.65	34.92	600	3.65	34.92	27.78

Station 2386; May 8; latitude 42°51′ N., longitude 51°03′ W.; depth 1,536 meters; dynamic height 971.030 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	1.13	33.24	0	1.13	33.24	26.65
25	.96	33.26	25	.96	33.26	26.67
49	—.37	33.34	50	—.40	33.34	26.81
74	—.90	33.54	75	—.90	33.54	27.00
99	—.88	33.58	100	—.85	33.58	27.01
148	—.38	33.72	150	—.35	33.73	27.11
197	—.04	33.81	200	0,00	33.82	27.18
296	1.26	34.14	300	1.35	34.17	27.38
395	3.04	34.60	400	3.05	34.61	27.59
593	3.60	34.88	600	3.65	34.88	27.74
791	3.78	34.93	800	3.80	34.93	27.77
1,004	3.68	34.94	1,000	3.70	34.94	27.79
1,390	3.53	34.95				

TABLE OF OCEANOGRAPHIC DATA—Continued

STATIONS OCCUPIED IN 1937—Continued

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
Station 2387; May 8; latitude 42°35′ N., longitude 51°25′ W.; depth 2,405 meters; dynamic height 970.946 meters						
0	3.34	33.47	0	3.35	33.47	26.66
25	1.26	33.52	25	1.26	33.52	26.86
50	1.45	33.76	50	1.45	33.76	27.04
76	.20	33.83	75	.20	33.83	27.17
101	.70	33.96	100	.70	33.96	27.25
151	1.09	34.10	150	1.05	34.10	27.34
202	2.98	34.41	200	2.95	34.40	27.43
303	3.08	34.64	300	3.05	34.63	27.60
406	3.36	34.78	400	3.35	34.77	27.69
608	4.10	34.94	600	4.10	34.94	27.75
809	3.84	34.95	800	3.85	34.95	27.78
1,024	3.64	34.925	1,000	3.65	34.93	27.78
1,411	3.56	34.93				
Station 2388; May 9; latitude 42°16′ N., longitude 51°44′ W.; depth 3,200 meters; dynamic height 971.131 meters						
0	13.94	35.21	0	13.94	35.21	26.38
24	13.62	35.28	25	13.65	35.28	26.49
48	13.09	35.27	50	13.05	35.27	26.61
72	12.74	35.22	75	12.75	35.22	26.64
96	12.59	35.32	100	12.55	35.32	26.75
144	12.15	35.34	150	12.05	35.34	26.86
193	11.33	35.36	200	11.20	35.36	27.04
289	8.65	35.14	300	8.20	35.09	27.33
338	6.70	34.88	400	5.10	34.79	27.51
504	3.76	34.75	600	3.75	34.80	27.67
668	3.78	34.86	800	4.10	34.95	27.76
871	4.18	34.965	1,000	3.95	34.96	27.78
1,273	3.22	34.96				
Station 2389; May 9; latitude 42°00′ N., longitude 52°00′ W.; depth 3,704 meters; dynamic height 971.189 meters						
0	15.47	35.48	0	15.47	35.48	26.25
25	15.15	35.58	25	15.16	35.58	26.40
50	14.01	35.50	50	14.02	35.50	26.59
76	13.42	35.45	75	13.45	35.45	26.67
101	13.29	35.43	100	13.30	35.43	26.68
151	13.06	35.52	150	13.05	35.52	26.81
201	12.42	35.49	200	12.45	35.49	26.90
302	9.69	35.24	300	9.75	35.25	27.20
330	9.43	35.21	400	7.80	35.13	27.42
496	6.26	35.03	600	5.35	35.01	27.66
661	4.99	35.01	800	4.55	35.00	27.75
849	4.40	35.00	1,000	4.10	34.99	27.79
1,220	3.81	34.97				
Station 2390; May 26; latitude 47°16′ N., longitude 45°05′ W.; depth 174 meters; dynamic height 970.869 meters						
0	7.69	34.32	0	7.69	34.32	26.81
25	5.68	34.38	25	5.68	34.38	27.12
50	4.34	34.42	50	4.34	34.42	27.31
75	3.79	34.42	75	3.79	34.42	27.37
100	3.58	34.45	100	3.58	34.45	27.41
150	3.48	34.56	150	3.48	34.56	27.51
Station 2391; May 27; latitude 47°26′ N., longitude 45°11′ W.; depth 220 meters; dynamic height 970.864 meters						
0	7.47	34.24	0	7.47	34.24	26.77
26	4.16	34.30	25	4.20	34.30	27.23
51	3.27	34.36	50	3.30	34.36	27.37
77	3.62	34.41	75	3.60	34.41	27.38
102	3.47	34.45	100	3.45	34.45	27.42
154	3.42	34.58	150	3.40	34.57	27.53
205	3.60	34.66	200	3.60	34.65	27.57
Station 2392; May 27; latitude 47°48′ N., longitude 45°24′ W.; depth 320 meters; dynamic height 970.873 meters						
0	7.29	34.18	0	7.29	34.18	26.75
25	5.29	34.18	25	5.29	34.18	27.01
50	4.08	34.30	50	4.08	34.30	27.24
75	3.74	34.38	75	3.74	34.38	27.34
125	3.54	34.50	100	3.60	34.44	27.40
176	3.75	34.65	150	3.60	34.57	27.51
276	3.92	34.85	200	3.85	34.71	27.59
			300	3.90	34.88	27.72
Station 2393; May 27; latitude 48°26′ N., longitude 45°40′ W.; depth 906 meters; dynamic height 970.817 meters						
0	6.69	34.32	0	6.69	34.32	26.95
25	3.88	34.44	25	3.88	34.44	27.37
51	3.39	34.60	50	3.40	34.60	27.55
76	3.29	34.65	75	3.30	34.65	27.60
101	3.05	34.64	100	3.05	34.64	27.61
152	2.99	34.73	150	3.00	34.72	27.69
203	3.52	34.83	200	3.50	34.83	27.72
304	3.68	34.90	300	3.70	34.90	27.76
407	3.42	34.87	400	3.45	34.87	27.76
601	3.59	34.91	600	3.60	34.91	27.78
807	3.35	34.92	800	3.35	34.92	27.81
Station 2394; May 27; latitude 48°45′ N., longitude 45°47′ W.; depth 1,637 meters; dynamic height 970.811 meters						
0	6.96	34.46	0	6.96	34.46	27.02
25	4.96	34.66	25	4.96	34.66	27.43
50	3.07	34.56	50	3.07	34.56	27.55
75	3.13	34.61	75	3.13	34.61	27.58
100	2.80	34.63	100	2.80	34.63	27.62
150	2.95	34.74	150	2.95	34.74	27.70
200	3.15	34.78	200	3.15	34.78	27.71
300	3.37	34.85	300	3.37	34.85	27.75
391	3.34	34.86	400	3.35	34.86	27.76
590	3.29	34.90	600	3.30	34.90	27.80
790	3.30	34.91	800	3.30	34.91	27.81
999	3.23	34.91	1,000	3.25	34.91	27.81
1,388	3.17	34.93				

TABLE OF OCEANOGRAPHIC DATA—Continued

STATIONS OCCUPIED IN 1937—Continued

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
Station 2395; May 27; latitude 48°37′ N., longitude 45°51′ W.; depth 1,161 meters; dynamic height 970.790 meters						
0	6.44	34.40	0	6.44	34.40	27.04
24	3.20	34.38	25	3.20	34.38	27.39
49	3.24	34.51	50	3.25	34.51	27.49
73	3.07	34.57	75	3.05	34.57	27.56
98	2.98	34.62	100	2.95	34.62	27.61
147	2.73	34.69	150	2.75	34.69	27.68
195	2.96	34.76	200	2.95	34.77	27.73
293	3.28	34.86	300	3.30	34.86	27.77
368	3.22	34.89	400	3.20	34.90	27.81
569	3.23	34.915	600	3.20	34.92	27.83
756	3.21	34.925	800	3.20	34.93	27.83
955	3.16	34.94	(1,000)	3.15	34.94	27.84
Station 2396; May 27; latitude 48°13′ N., longitude 46°02′ W.; depth 1,088 meters; dynamic height 970.824 meters						
0	7.14	34.05	0	7.14	34.05	26.67
26	2.80	34.18	25	2.90	34.17	27.26
51	2.49	34.39	50	2.50	34.37	27.45
77	2.80	34.55	75	2.75	34.54	27.56
102	3.24	34.69	100	3.20	34.68	27.63
153	3.31	34.76	150	3.30	34.75	27.68
205	3.23	34.80	200	3.25	34.80	27.72
307	3.71	34.90	300	3.70	34.90	27.76
405	3.67	34.91	400	3.70	34.91	27.77
618	3.57	34.92	600	3.60	34.92	27.79
811	3.52	34.92	800	3.55	34.92	27.79
1,010	3.27	34.95	1,000	3.30	34.95	27.84
Station 2397; May 27; latitude 47°47′ N.; longitude 46°11′ W.; depth 923 meters; dynamic height 970.823 meters						
0	7.08	33.90	0	7.08	33.90	26.56
26	3.01	34.11	25	3.10	34.10	27.18
51	1.99	34.33	50	2.00	34.32	27.45
77	2.24	34.48	75	2.20	34.47	27.56
102	3.33	34.69	100	3.30	34.66	27.61
153	3.31	34.78	150	3.30	34.78	27.70
205	3.33	34.82	200	3.35	34.82	27.73
307	3.34	34.86	300	3.35	34.86	27.76
416	3.45	34.90	400	3.45	34.89	27.77
608	3.56	34.93	600	3.55	34.93	27.79
809	3.51	34.945	800	3.50	34.94	27.81
Station 2398; May 28; latitude 47°22′ N., longitude 46°06′ W.; depth 375 meters; dynamic height 970.855 meters						
0	7.47	34.14	0	7.47	34.14	26.70
26	5.11	34.37	25	5.15	34.36	27.17
51	3.87	34.39	50	3.90	34.39	27.33
77	3.49	34.41	75	3.50	34.41	27.39
103	3.11	34.44	100	3.15	34.44	27.44
154	3.54	34.66	150	3.50	34.65	27.58
205	3.63	34.76	200	3.60	34.75	27.65
308	3.64	34.88	300	3.65	34.87	27.74

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
Station 2399; May 28; latitude 47°18′ N., longitude 47°16′ W.; depth 686 meters; dynamic height 970.844 meters						
0	4.70	33.26	0	4.70	33.26	26.35
25	.62	33.81	25	.62	33.81	27.13
51	.58	34.06	50	.60	34.05	27.32
76	1.12	34.23	75	1.15	34.22	27.43
102	1.47	34.36	100	1.40	34.35	27.52
153	2.26	34.54	150	2.20	34.53	27.60
203	2.44	34.63	200	2.40	34.62	27.66
306	2.77	34.73	300	2.75	34.73	27.71
400	3.00	34.80	400	3.00	34.80	27.75
600	3.26	34.89	600	3.25	34.89	27.79
Station 2400; May 28; latitude 47°50′ N., longitude 47°18′ W.; depth 308 meters; dynamic height 970.855 meters						
0	5.52	32.26	0	5.52	32.26	25.47
25	.56	33.78	25	.56	33.78	27.11
51	.57	34.04	50	.55	34.03	27.31
76	.78	34.16	75	.75	34.15	27.40
102	1.16	34.26	100	1.10	34.25	27.46
153	2.75	34.60	150	2.70	34.59	27.60
203	2.82	34.71	200	2.80	34.71	27.69
295	2.98	34.77	300	3.00	34.77	27.73
Station 2401; May 28; latitude 48°15′ N.; longitude 47°22′ W.; depth, 1,719 meters; dynamic height 970.826 meters						
0	6.11	33.08	0	6.11	33.08	26.05
25	2.89	34.01	25	2.89	34.01	27.13
51	2.16	34.30	50	2.20	34.29	27.41
76	2.02	34.42	75	2.00	34.42	27.53
102	2.19	34.48	100	2.15	34.47	27.56
153	2.66	34.66	150	2.60	34.65	27.66
203	3.05	34.78	200	3.05	34.77	27.72
305	3.14	34.82	300	3.15	34.82	27.75
408	3.14	34.86	400	3.15	34.85	27.77
611	3.26	34.92	600	3.25	34.92	27.82
813	3.31	34.93	800	3.30	34.93	27.82
1,025	3.33	34.96	1,000	3.35	34.96	27.84
1,418	3.21	34.94				
Station 2402; May 28; latitude 48°08′ N., longitude 47°40′ W.; depth 878 meters; dynamic height 970.791 meters						
0	6.12	33.59	0	6.12	33.59	26.45
25	2.45	34.34	25	2.45	34.34	27.42
51	2.25	34.51	50	2.25	34.51	27.58
76	2.38	34.60	75	2.35	34.60	27.64
102	2.70	34.66	100	2.65	34.66	27.67
153	2.96	34.72	150	2.95	34.71	27.68
203	2.90	34.79	200	2.90	34.79	27.74
305	3.19	34.87	300	3.20	34.87	27.79
416	3.26	34.89	400	3.25	34.89	27.80
609	3.28	34.91	600	3.25	34.91	27.82
810	3.31	34.94	800	3.30	34.94	27.83

TABLE OF OCEANOGRAPHIC DATA—Continued

STATIONS OCCUPIED IN 1937—Continued

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
Station 2403; May 28; latitude 48°05′ N., longitude 47°45′ W.; depth 631 meters; dynamic height 970.805 meters						
0	4.70	32.08	0	4.70	32.08	25.42
25	2.75	34.24	25	2.75	34.24	27.32
51	1.96	34.36	50	1.95	34.35	27.48
76	2.15	34.49	75	2.15	34.49	27.57
102	2.34	34.60	100	2.30	34.59	27.64
153	2.73	34.74	150	2.70	34.73	27.71
203	3.00	34.80	200	3.00	24.80	27.75
305	3.22	34.89	300	3.20	34.88	27.79
408	3.23	34.91	400	3.25	34.91	27.81
610	3.30	34.94	600	3.30	34.94	27.83
Station 2404; May 28; latitude 47°54′ N., longitude 48°10′ W.; depth 320 meters; dynamic height 970.852 meters						
0	4.20	32.03	0	4.20	32.03	25.44
25	.84	33.63	25	.84	33.63	26.97
51	−.65	33.82	50	−.65	33.82	27.21
76	.27	34.00	75	.25	34.00	27.31
102	1.20	34.25	100	1.10	34.23	27.44
153	1.99	34.48	150	1.95	34.47	27.58
204	2.42	34.60	200	2.40	34.59	27.63
306	3.14	34.83	300	3.10	34.82	27.76
Station 2405; May 29; latitude 47°33′ N., longitude 48°55′ W.; depth 165 meters; dynamic height 970.937 meters						
0	3.22	32.32	0	3.22	32.32	25.75
26	.50	32.99	25	.55	32.98	26.47
52	−1.44	33.21	50	−1.40	33.19	26.72
78	−.84	33.41	75	−.85	33.40	26.87
104	−.95	33.52	100	−.95	33.50	26.96
156	−.06	33.88	150	−.15	33.83	27.19
Station 2406; May 29; latitude 47°24′ N., longitude 49°13′ W.; depth 125 meters; dynamic height 970.930 meters						
0	4.90	32.90	0	4.90	32.90	26.04
26	.87	33.01	25	1.00	33.00	26.47
52	−1.10	33.26	50	−.95	33.23	26.74
78	−1.44	33.47	75	−1.45	33.43	26.92
104	−.94	33.60	100	−1.05	33.58	27.02
Station 2407; May 29; latitude 47°18′ N., longitude 49°22′ W.; depth 89 meters; dynamic height 970.933 meters						
0	4.97	32.87	0	4.97	32.87	26.02
26	1.04	33.00	25	1.10	32.99	26.45
53	−1.29	33.15	50	−1.25	33.13	26.66
79	−.92	33.48	75	−1.00	33.42	26.90
Station 2408; May 29; latitude 46°55′ N., longitude 48°46′ W.; depth 88 meters; dynamic height 970.967 meters						
0	5.83	33.04	0	5.83	33.04	26.05
26	1.31	33.04	25	1.40	33.04	26.47
53	−.44	33.14	50	−.40	33.12	26.63
79	−.39	33.49	75	−.40	33.44	26.89
Station 2409; May 29; latitude 46°54′ N., longitude 48°17′ W.; depth 115 meters; dynamic height 970.962 meters						
0	4.98	32.99	0	4.98	32.99	26.11
26	.39	33.08	25	.50	33.08	26.55
51	−1.00	33.28	50	−.95	33.28	26.78
77	−1.37	33.40	75	−1.35	33.39	26.88
103	−.80	33.58	100	−.95	33.56	27.01
Station 2410; May 29; latitude 46°53′ N., longitude 47°46′ W.; depth 165 meters; dynamic height 970.964 meters						
0	4.46	32.99	0	4.46	32.99	26.16
26	1.41	33.15	25	1.45	33.15	26.56
51	.97	33.32	50	1.00	33.31	26.71
77	−1.19	33.42	75	−1.15	33.41	26.90
103	−1.28	33.52	100	−1.30	33.50	26.97
154	−.32	33.82	150	−.45	33.79	27.17
Station 2411; May 29–30; latitude 46°53′ N., longitude 47°16′ W.; depth 631 meters; dynamic height 970.881 meters						
0	4.62	32.68	0	4.62	32.68	25.90
25	1.18	33.78	25	1.18	33.78	27.07
51	−.08	33.90	50	−.05	33.89	27.23
76	.95	34.15	75	.95	34.14	27.37
102	1.35	34.28	100	1.30	34.26	27.46
153	2.23	34.52	150	2.20	34.51	27.59
204	2.50	34.62	200	2.50	34.61	27.64
306	2.92	34.74	300	2.90	34.73	27.70
406	3.04	34.78	400	3.05	34.77	27.72
607	3.32	34.86	600	3.30	34.86	27.77
Station 2412; May 30; latitude 46°52′ N., longitude 47°04′ W.; depth 1,188 meters; dynamic height 970.845 meters						
0	7.24	33.93	0	7.24	33.93	26.56
25	1.90	34.01	25	1.90	34.01	27.21
51	2.19	34.27	50	2.20	34.25	27.38
76	2.24	34.43	75	2.25	34.43	27.51
102	2.41	34.54	100	2.40	34.53	27.58
153	2.90	34.69	150	2.90	34.68	27.66
204	3.05	34.76	200	3.05	34.75	27.70
306	3.33	34.84	300	3.30	34.83	27.74
405	3.37	34.86	400	3.35	34.86	27.76
611	3.48	34.89	600	3.45	34.89	27.77
793	3.44	34.91	800	3.45	34.91	27.79
994	3.42	34.93	1,000	3.45	34.93	27.80
Station 2413; May 30; latitude 46°51′ N., longitude 46°34′ W.; depth 631 meters; dynamic height 970.859 meters						
0	7.97	34.23	0	7.97	34.23	26.69
25	4.54	34.33	25	4.54	34.33	27.21
51	3.78	34.39	50	3.80	34.39	27.34
76	3.49	34.44	75	3.50	34.44	27.41
102	3.51	34.50	100	3.50	34.49	27.45
153	3.65	34.65	150	3.65	34.64	27.55
203	3.78	34.74	200	3.75	34.73	27.61
305	3.64	34.86	300	3.65	34.85	27.72
392	3.68	34.91	400	3.70	34.91	27.77
588	3.56	34.92	600	3.55	34.92	27.79

TABLE OF OCEANOGRAPHIC DATA—Continued

STATIONS OCCUPIED IN 1937—Continued

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
Station 2414; May 30; latitude 46°51′ N., longitude 46°17′ W.; depth 326 meters; dynamic height 970.857 meters						
0	9.00	34.00	0	9.00	34.00	26.36
25	5.40	34.41	25	5.40	34.41	27.18
50	3.65	34.36	50	3.65	34.36	27.33
76	3.49	34.46	75	3.50	34.46	27.43
101	3.60	34.56	100	3.60	34.56	27.50
151	3.64	34.68	150	3.60	34.68	27.59
202	3.69	34.74	200	3.70	34.73	27.62
303	3.65	34.87	300	3.65	34.87	27.74
Station 2415; May 30; latitude 46°50′ N., longitude 45°28′ W.; depth 229 meters; dynamic height 970.858 meters						
0	8.97	33.85	0	8.97	33.85	26.25
26	5.54	34.40	25	5.55	34.38	27.14
52	4.57	34.51	50	4.65	34.51	27.35
78	3.51	34.48	75	3.50	34.48	27.44
104	3.78	34.58	100	3.75	34.57	27.49
155	3.74	34.67	150	3.75	34.66	27.56
207	3.73	34.73	200	3.70	34.72	27.62
Station 2416; May 30; latitude 46°49′ N., longitude 45°00′ W.; depth 165 meters; dynamic height 970.867 meters						
0	9.60	34.02	0	9.60	34.02	26.27
26	5.22	34.31	25	5.30	34.31	27.12
53	3.60	34.31	50	3.70	34.31	27.29
79	3.46	34.38	75	3.45	34.37	27.36
106	3.40	34.44	100	3.40	34.43	27.41
159	3.57	34.58	150	3.50	34.56	27.51
Station 2417; May 30; latitude 46°49′ N., longitude 44°42′ W.; depth 146 meters; dynamic height 970.860 meters						
0	7.60	34.18	0	7.60	34.18	26.70
26	4.94	34.36	25	5.00	34.36	27.19
53	3.96	34.42	50	4.00	34.41	27.34
79	3.79	34.47	75	3.80	34.46	27.40
106	3.56	34.48	100	3.60	34.48	27.43
Station 2418; May 30; latitute 47°45′ N., longitude 44°43′ W.; depth 185 meters; dynamic height 970.872 meters						
0	7.95	34.16	0	7.95	34.16	26.64
26	4.94	34.24	25	5.00	34.24	27.09
52	3.67	34.30	50	3.70	34.29	27.27
79	3.62	34.40	75	3.65	34.38	27.35
105	3.59	34.47	100	3.60	34.46	27.42
157	3.54	34.54	150	3.55	34.53	27.47
Station 2419; May 30; latitude 46°39′ N., longitude 44°43′ W.; depth 225 meters; dynamic height 970.877 meters						
0	9.56	34.11	0	9.56	34.11	26.35
26	5.69	34.19	25	5.80	34.19	26.96
51	3.74	34.27	50	3.80	34.29	27.25
77	3.52	34.35	75	3.55	34.34	27.32
103	3.42	34.45	100	3.45	34.43	27.40
154	3.57	34.62	150	3.55	34.61	27.54
206	3.77	34.74	200	3.75	34.73	27.61
Station 2420; May 30; latitude 46°32′ N., longitude 44°44′ W.; depth 714 meters; dynamic height 970.879 meters						
0	11.18	34.12	0	11.18	34.12	26.08
24	5.95	34.20	25	5.90	34.20	26.95
48	3.64	34.32	50	3.65	34.33	27.31
73	3.62	34.38	75	3.65	34.39	27.35
97	3.47	34.44	100	3.45	34.45	27.42
145	3.34	34.53	150	3.35	34.55	27.51
193	3.61	34.68	200	3.60	34.69	27.60
290	3.69	34.86	300	3.70	34.87	27.74
377	3.78	34.90	400	3.75	34.90	27.75
577	3.70	34.92	600	3.70	34.92	27.78
Station 2421; May 31; latitude 46°26′ N.; longitude 44°45′ W.; depth 1,829 meters; dynamic height 970.887 meters						
0	11.02	34.14	0	11.02	34.14	26.12
25	4.19	33.71	25	4.19	33.71	26.77
51	3.46	34.11	50	3.45	34.09	27.13
76	4.28	34.39	75	4.25	34.38	27.28
101	4.83	34.60	100	4.85	34.60	27.40
152	4.12	34.66	150	4.10	34.66	27.53
203	4.19	34.80	200	4.20	34.80	27.63
304	4.12	34.88	300	4.10	34.88	27.70
384	3.88	34.91	400	3.85	34.92	27.76
579	3.62	34.92	600	3.60	34.92	27.79
775	3.43	34.91	800	3.40	34.91	27.80
983	3.36	34.92	1,000	3.35	34.92	27.81
1,368	3.30	34.92				
Station 2422; May 31; latitude 46°02′ N.; longitude 44°48′ W.; depth 3,713 meters; dynamic height 970.901 meters						
0	11.29	34.15	0	11.29	34.15	26.08
26	6.26	34.21	25	6.30	34.21	26.91
51	4.16	34.23	50	4.15	34.23	27.18
77	4.27	34.39	75	4.25	34.38	27.28
103	4.54	34.58	100	4.50	34.55	27.40
154	5.57	34.90	150	5.50	34.90	27.56
205	4.17	34.75	200	4.30	34.75	27.58
308	4.72	34.96	300	4.70	34.95	27.69
394	4.34	34.94	400	4.35	34.94	27.72
594	4.20	34.99	600	4.20	34.99	27.78
795	3.83	34.97	800	3.85	34.97	27.80
1,011	3.71	34.96	1,000	3.75	34.96	27.80
1,393	3.39	34.94				
Station 2423; May 31; latitude 46°05′ N.; longitude 45°24′ W.; depth 2,533 meters; dynamic height 970.876 meters						
0	9.47	33.98	0	9.47	33.98	26.26
25	4.51	34.12	25	4.51	34.12	27.06
51	3.83	34.30	50	3.85	34.30	27.27
76	4.12	34.47	75	4.10	34.46	27.37
102	4.14	34.60	100	4.15	34.59	27.46
153	4.05	34.70	150	4.05	34.69	27.55
203	4.56	34.86	200	4.55	34.85	27.63
305	4.62	34.96	300	4.60	34.96	27.71
375	4.34	34.96	400	4.25	34.96	27.75
565	3.99	34.95	600	3.95	34.95	27.77
757	3.82	34.97	800	3.80	34.97	27.81
953	3.63	34.95	1,000	3.60	34.95	27.81
1,353	3.32	34.93				

TABLE OF OCEANOGRAPHIC DATA—Continued

STATIONS OCCUPIED IN 1937—Continued

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
Station 2424; May 31; latitude 46°08′ N.; longitude 45°58′ W.; depth 1,362 meters; dynamic height 970.870 meters						
0	9.33	34.05	0	9.33	34.05	26.34
22	5.93	34.20	25	5.85	34.23	26.98
45	4.69	34.29	50	4.55	34.30	27.19
67	3.79	34.32	75	4.00	34.36	27.30
89	4.33	34.52	100	4.40	34.58	27.43
134	4.46	34.69	150	4.40	34.72	27.54
178	4.17	34.76	200	4.10	34.79	27.63
267	4.12	34.88	300	4.45	34.99	27.75
295	4.46	34.98	400	4.40	35.02	27.78
449	4.38	35.02	600	4.15	35.00	27.79
607	4.12	35.00	800	3.85	34.99	27.81
781	3.87	34.99	1,000	3.50	34.95	27.82
1,057	3.40	34.94				
Station 2425; May 31; latitude 46°13′ N., longitude 46°34′ W.; depth 951 meters; dynamic height 970.851 meters						
0	7.97	33.96	0	7.97	33.96	26.49
24	5.03	34.37	25	5.00	34.37	27.20
49	3.82	34.38	50	3.80	34.38	27.33
73	3.46	34.45	75	3.45	34.46	27.43
97	3.61	34.53	100	3.60	34.54	27.48
146	3.58	34.66	150	3.55	34.67	27.59
194	3.85	34.82	200	3.85	34.82	27.68
291	3.70	34.86	300	3.70	34.86	27.73
339	3.71	34.90	400	3.70	34.92	27.78
525	3.70	34.93	600	3.70	34.93	27.78
721	3.62	34.935	(800)	3.60	34.94	27.80
Station 2426; May 31; latitude 46°15 N., longitude 46°54′ W.; depth 1,115 meters; dynamic height 970.826 meters						
0	6.62	33.96	0	6.62	33.96	26.67
26	4.20	34.13	25	4.25	34.12	27.08
51	2.57	34.33	50	2.60	34.31	27.39
77	2.54	34.48	75	2.55	34.47	27.53
103	2.89	34.64	100	2.85	34.62	27.62
154	3.15	34.74	150	3.10	34.73	27.68
205	3.41	34.82	200	3.40	34.81	27.72
308	3.56	34.90	300	3.55	34.90	27.77
400	*3.55	34.91	400	3.55	34.91	27.78
599	3.57	34.925	600	3.55	34.93	27.79
798	3.46	34.935	800	3.45	34.94	27.81
996	3.34	34.935	1,000	3.35	34.94	27.82
Station 2427; June 1; latitude 46°18′ N., longitude 47°13′ W.; depth 622 meters; dynamic height 970.849 meters						
0	4.73	32.66	0	4.73	32.66	25.87
26	.36	33.80	25	.35	33.78	27.12
51	.55	34.03	50	.55	34.03	27.31
77	1.45	34.24	75	1.30	34.23	27.42
102	1.80	34.38	100	1.80	34.36	27.50
153	2.65	34.63	150	2.60	34.62	27.64
205	2.92	34.71	200	2.90	34.70	27.68
307	3.15	34.80	300	3.15	34.80	27.73
408	3.17	34.85	400	3.15	34.85	27.77
608	3.42	34.91	600	3.40	34.91	27.80

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
Station 2428; June 1; latitude 46°21′ N., longitude 47°39′ W.; depth 165 meters; dynamic height 970.921 meters						
0	4.35	32.94	0	4.35	32.94	26.13
25	−.82	33.27	25	−.82	33.27	26.76
51	−.96	33.48	50	−.95	33.47	26.94
76	−.76	33.66	75	−.75	33.66	27.08
102	−.23	33.84	100	−.25	33.82	27.19
153	.17	33.96	150	.15	33.95	27.27
Station 2429; June 1; latitude 46°24′ N., longitude 48°01′ W.; depth 115 meters; dynamic height 970.942 meters						
0	5.65	32.94	0	5.65	32.94	25.99
26	.71	33.08	25	.80	33.08	26.54
52	−.93	33.30	50	−.80	33.28	26.77
79	−1.07	33.46	75	−1.05	33.43	26.90
105	−.43	33.69	100	−.60	33.65	27.06
Station 2430; June 1; latitude 46°27′ N., longitude 48°34′ W.; depth 88 meters; dynamic height 970.946 meters						
0	6.19	33.00	0	6.19	33.00	25.97
26	1.31	33.06	25	1.40	33.06	26.48
53	−.41	33.14	50	−.40	33.13	26.64
79	−.39	33.58	75	−.40	33.49	26.93
Station 2431; June 1; latitude 46°23′ N., longitude 49°00′ W.; depth 65 meters; dynamic height 970.963 meters						
0	6.50	33.05	0	6.50	33.05	25.96
27	2.89	33.19	25	3.10	33.18	26.45
54	.10	33.32	50	.35	33.30	26.73
Station 2432; June 1; latitude 46°06′ N., longitude 48°33′ W.; depth 88 meters; dynamic height 970.984 meters						
0	6.50	32.97	0	6.50	32.97	25.91
26	.61	33.04	25	.70	33.04	26.51
53	−.94	33.16	50	−.90	33.14	26.67
79	−.23	33.63	75	−.35	33.56	26.98
Station 2433; June 1; latitude 45°51′ N., longitude 48°10′ W.; depth 110 meters; dynamic height 970.974 meters						
0	5.49	32.94	0	5.49	32.94	26.01
26	−1.05	33.22	25	−1.05	33.22	26.73
52	−.84	33.37	50	−.85	33.35	26.82
78	−1.22	33.50	75	−1.20	33.49	26.96
104	−.77	33.59	100	−.85	33.57	27.01
Station 2434; June 1; latitude 45°48′ N., longitude 48°05′ W.; depth 169 meters; dynamic height 970.961 meters						
0	4.80	32.78	0	4.80	32.78	25.96
26	−.04	33.25	25	−.05	33.24	26.71
52	.42	33.57	50	.40	33.55	26.94
78	−.28	33.70	75	−.30	33.69	27.08
104	.13	33.89	100	.05	33.86	27.21
156	.79	34.11	150	.70	34.09	27.35

TABLE OF OCEANOGRAPHIC DATA—Continued

STATIONS OCCUPIED IN 1937—Continued

Station 2435; June 1; latitude 45°42′ N., longitude 47°55′ W.; depth 622 meters; dynamic height 970.928 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	4.83	32.91	0	4.83	32.91	26.06
25	2.12	33.08	25	2.12	33.08	26.45
49	.99	33.63	50	.95	33.64	26.97
74	−.45	33.72	75	−.45	33.72	27.12
99	.17	33.96	100	.20	33.98	27.29
148	1.63	34.36	150	1.65	34.37	27.52
197	1.96	34.44	200	2.00	34.44	27.54
296	2.41	34.59	300	2.45	34.60	27.63
396	3.25	34.82	400	3.25	34.82	27.74
593	3.18	34.83	600	3.15	34.83	27.75

Station 2436; June 2; latitude 45°38′ N., longitude 47°49′ W.; depth 1,097 meters; dynamic height 970.899 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	5.11	33.14	0	5.11	33.14	26.22
24	3.36	33.45	25	3.30	33.46	26.65
48	.52	33.72	50	.45	33.74	27.08
71	.28	33.87	75	.25	33.89	27.22
95	.35	34.00	100	.50	34.04	27.32
143	1.90	34.34	150	2.00	34.38	27.49
190	2.63	34.57	200	2.70	34.60	27.61
285	3.22	34.78	300	3.25	34.80	27.72
330	3.28	34.82	400	3.25	34.84	27.75
510	3.21	34.84	600	3.35	34.87	27.77
701	3.50	34.90	800	3.50	34.91	27.79
894	3.44	34.92	(1,000)	3.40	34.92	27.81

Station 2437; June 2; latitude 45°31′ N., longitude 47°38′ W.; depth 1,511 meters; dynamic height 970.899 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	10.73	33.90	0	10.73	33.90	25.98
23	5.15	33.58	25	4.75	33.58	26.60
46	.94	33.74	50	.95	33.77	27.08
69	1.04	33.97	75	1.10	34.01	27.27
92	1.58	34.12	100	1.75	34.19	27.36
138	3.65	34.60	150	3.75	34.64	27.54
184	3.94	34.71	200	4.00	34.74	27.60
276	4.39	34.90	300	4.00	34.87	27.71
327	3.65	34.85	400	3.75	34.90	27.75
501	3.97	34.95	600	3.85	34.97	27.80
682	3.79	34.97	800	3.65	34.95	27.80
865	3.60	34.94	1,000	3.55	34.94	27.80
1,249	3.35	34.935				

Station 2438; June 2; latitude 45°20′ N., longitude 47°21′ W.; depth 2,761 meters; dynamic height 970.907 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	11.52	34.02	0	11.52	34.02	25.94
23	9.10	34.07	25	8.60	34.07	26.48
47	2.70	33.82	50	2.50	33.82	27.01
70	1.81	33.96	75	1.85	34.01	27.21
93	2.50	34.20	100	2.60	34.25	27.34
140	3.14	34.51	150	3.25	34.56	27.53
187	3.60	34.70	200	3.75	34.74	27.62
280	4.39	34.92	300	4.35	34.92	27.71
320	4.32	34.92	400	4.30	34.96	27.74
484	4.20	34.98	600	4.00	34.98	27.79
651	3.89	34.97	800	3.65	34.95	27.80
832	3.58	34.95	1,000	3.50	34.95	27.82
1,214	3.46	34.96				

Station 2439; June 2; latitude 45°17′ N., longitude 46°38′ W.; depth 3,237 meters; dynamic height 970.877 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	9.33	34.02	0	9.33	34.02	26.32
24	6.80	34.24	25	6.75	34.25	26.88
48	4.91	34.41	50	4.80	34.42	27.26
64	4.53	34.50	75	4.50	34.50	27.36
95	4.41	34.62	100	4.40	34.63	27.47
143	4.20	34.70	150	4.15	34.71	27.56
191	3.90	34.78	200	3.90	34.79	27.65
286	3.86	34.87	300	3.85	34.88	27.72
335	3.81	34.89	400	3.75	34.90	27.75
517	3.65	34.91	600	3.60	34.91	27.78
707	3.60	34.92	800	3.60	34.92	27.79
895	3.51	34.93	1,000	3.50	34.93	27.80
1,285	3.32	34.93				

Station 2440; June 2; latitude 45°16′ N., longitude 45°55′ W.; depth 3,484 meters; dynamic height 970.883 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
15	7.66	33.95	0	9.30	33.78	26.13
41	4.87	34.34	25	6.35	34.08	26.80
66	4.73	34.50	50	4.80	34.41	27.25
84	4.72	34.56	75	4.75	34.53	27.35
117	4.28	34.66	100	4.50	34.61	27.44
168	4.20	34.74	150	4.20	34.71	27.56
219	4.89	34.95	200	4.70	34.87	27.63
321	3.88	34.87	300	3.95	34.88	27.71
409	4.33	34.99	400	4.35	34.98	27.75
613	3.62	34.93	600	3.65	34.93	27.78
816	3.48	34.93	800	3.50	34.93	27.80
1,018	3.44	34.94	1,000	3.45	34.94	27.81
1,418	3.24	34.93				

Station 2441; June 2–3; latitude 44°45′ N., longitude 46°11′ W.; depth 3,466 meters; dynamic height 970.920 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	11.00	33.94	0	11.00	33.94	25.97
24	4.24	33.69	25	4.20	33.69	26.75
48	2.61	33.88	50	2.65	33.94	27.09
64	5.58	34.48	75	6.00	34.62	27.28
96	6.33	34.73	100	6.35	34.74	27.32
144	5.98	34.80	150	5.85	34.80	27.43
192	4.08	34.62	200	4.10	34.62	27.50
288	4.41	34.86	300	4.35	34.87	27.67
352	4.03	34.88	400	3.85	34.89	27.73
534	3.57	34.90	600	3.55	34.91	27.78
721	3.54	34.92	800	3.55	34.93	27.79
912	3.49	34.93	1,000	3.50	34.93	27.80
1,307	3.36	34.93				

Station 2442; June 3; latitude 44°15′ N., longitude 46°28′ W.; depth 3,859 meters; dynamic height 971.215 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	15.98	35.55	0	15.98	35.55	26.19
26	15.74	35.53	25	15.75	35.53	26.23
51	13.80	35.52	50	13.95	35.52	26.62
68	13.46	35.47	75	13.50	35.49	26.69
103	13.63	35.60	100	13.65	35.58	26.73
154	13.60	35.72	150	13.60	35.72	26.85
205	12.65	35.61	200	12.75	35.62	26.94
308	11.09	35.43	300	11.25	35.44	27.09
411	8.08	35.06	400	8.35	35.09	27.31
612	5.24	34.98	600	5.35	34.98	27.63
810	4.03	34.95	800	4.05	34.95	27.76
1,012	3.63	34.92	1,000	3.65	34.92	27.78
1,418	3.47	34.94				

TABLE OF OCEANOGRAPHIC DATA—Continued

STATIONS OCCUPIED IN 1937—Continued

Station 2443; June 3; latitude 44°22′ N., longitude 47°06′ W.; depth 3,978 meters; dynamic height 971.210 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	15.99	35.55	0	15.99	35.55	26.19
26	15.81	35.55	25	15.85	35.55	26.22
51	13.86	35.50	50	13.90	35.50	26.61
69	13.87	35.59	75	13.80	35.58	26.69
102	13.16	35.52	100	13.20	35.52	26.77
153	13.00	35.59	150	13.00	35.59	26.86
205	12.44	35.59	200	12.50	35.59	26.96
307	10.81	35.41	300	11.00	35.43	27.13
402	8.31	35.10	400	8.45	35.11	27.31
604	5.41	34.99	600	5.45	34.99	27.63
807	3.85	34.91	800	3.85	34.91	27.75
1,005	3.75	34.94	1,000	3.75	34.94	27.78
1,397	3.61	34.955				

Station 2444; June 3; latitude 44°32′ N., longitude 47°42′ W.; depth 3,530 meters; dynamic height 971.006 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	11.48	34.07	0	11.48	34.07	25.99
25	8.20	33.81	25	8.20	33.81	26.33
50	5.33	33.93	50	5.34	33.93	26.81
66	1.57	33.65	75	1.80	33.70	26.97
99	3.16	33.99	100	3.30	34.03	27.10
149	6.35	34.65	150	6.35	34.65	27.25
199	6.08	34.69	200	6.05	34.69	27.32
298	4.52	34.69	300	4.50	34.69	27.50
401	4.49	34.88	400	4.50	34.88	27.65
602	4.19	34.96	600	4.20	34.96	27.76
805	3.91	34.97	800	3.90	34.97	27.80
1,005	3.70	34.96	1,000	3.70	34.96	27.81
1,406	3.36	34.95				

Station 2445; June 3; latitude 44°42′ N., longitude 48°19′ W.; depth 2,889 meters; dynamic height 970.922 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	8.66	33.76	0	8.66	33.76	26.22
26	7.33	33.80	25	7.40	33.80	26.44
51	4.16	33.95	50	4.30	33.94	26.93
69	2.96	33.98	75	3.00	34.02	27.13
103	3.38	34.26	100	3.35	34.23	27.25
154	3.51	34.54	150	3.50	34.52	27.48
205	3.95	34.74	200	3.95	34.72	27.59
308	4.37	34.92	300	4.35	34.91	27.70
406	4.26	34.96	400	4.30	34.96	27.74
611	3.72	34.93	600	3.75	34.93	27.77
818	3.77	34.96	800	3.75	34.96	27.80
1,019	3.55	34.95	1,000	3.55	34.95	27.81
1,419	3.34	34.94				

Station 2446; June 4; latitude 44°50′ N., longitude 48°46′ W.; depth 1,463 meters; dynamic height 970.892 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	5.92	33.30	0	5.92	33.30	26.24
25	2.87	33.88	25	2.87	33.88	27.02
51	2.45	34.09	50	2.45	34.08	27.21
67	2.26	34.20	75	2.00	34.18	27.33
102	−.29	34.00	100	−.30	34.00	27.33
153	1.88	34.21	150	1.80	34.19	27.36
204	2.19	34.46	200	2.15	34.43	27.52
306	3.61	34.90	300	3.60	34.89	27.76
403	3.55	34.88	400	3.55	34.88	27.75
606	3.45	34.89	600	3.45	34.89	27.77
810	3.52	34.93	800	3.50	34.93	27.80
1,011	3.48	34.94	1,000	3.50	34.94	27.81
1,412	3.35	34.94				

Station 2447; June 4; latitude 44°53′ N., longitude 48°58′ W.; depth 622 meters; dynamic height 970.957 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	5.05	32.96	0	5.05	32.96	26.07
25	−1.05	33.33	25	−1.05	33.33	26.82
51	−.80	33.58	50	−.80	33.57	27.01
70	−.60	33.67	75	−.55	33.68	27.08
102	−.41	33.76	100	−.45	33.75	27.14
153	.27	33.97	150	.20	33.95	27.27
203	1.48	34.32	200	1.40	34.30	27.48
305	2.51	34.62	300	2.50	34.61	27.64
404	2.82	34.72	400	2.85	34.72	27.70
610	3.02	34.78	600	3.00	34.78	27.73

Station 2448; June 4; latitude 44°43′ N., longitude 49°01.5′ W.; depth 224 meters; dynamic height 970.996 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	5.02	32.95	0	5.02	32.95	26.08
25	−1.29	33.43	25	−1.29	33.43	26.91
51	−.97	33.54	50	−.95	33.54	26.99
76	−1.07	33.57	75	−1.05	33.57	27.02
101	−.83	33.63	100	−.85	33.63	27.05
152	−.31	33.80	150	−.35	33.78	27.15
203	1.08	34.23	200	.90	34.18	27.41

Station 2449; June 4; latitude 44°55′ N., longitude 49°07′ W.; depth 88 meters; dynamic height 970.983 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	4.97	32.96	0	4.97	32.96	26.09
26	−.33	33.18	25	−.25	33.18	26.67
51	−1.23	33.28	50	−1.25	33.27	26.78
77	−1.02	33.45	75	−1.05	33.44	26.91

Station 2450; June 4; latitude 45°02′ N., longitude 49°29′ W.; depth 64 meters; dynamic height 970.980 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	6.08	33.08	0	6.08	33.08	26.05
26	.48	33.25	25	.60	33.25	26.68
52	−.59	33.44	50	−.50	33.42	26.88

Station 2,451; June 4; latitude 44°12′ N., longitude 49°46′ W.; depth 40 meters; dynamic height 971.005 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	8.05	33.06	0	8.05	33.06	25.76
16	6.27	33.02	25	4.40	33.05	26.22
32	2.62	33.10	(40)	1.40	33.13	26.54

Station 2452; June 4; latitude 43°57′ N., longitude 49°08′ W.; depth 87 meters; dynamic height 970.986 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	4.52	33.08	0	4.52	33.08	26.23
26	−.01	33.24	25	.00	33.24	26.71
53	−1.01	33.43	50	−1.00	33.41	26.89
79	−.85	33.54	75	−.90	33.53	26.98

TABLE OF OCEANOGRAPHIC DATA—Continued

STATIONS OCCUPIED IN 1937—Continued

Station 2453; June 4; latitude 43°55′ N., longitude 48°58′ W.; depth 622 meters; dynamic height 970.953 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	4.33	33.00	0	4.33	33.00	26.18
25	−.50	33.30	25	−.50	33.30	26.77
50	−.88	33.55	50	−.88	33.55	26.99
67	−.72	33.61	75	−.65	33.64	27.06
100	−.51	33.69	100	−.51	33.69	27.09
150	−.09	33.85	150	−.09	33.85	27.20
201	1.50	34.30	200	1.45	34.29	27.46
301	2.75	34.70	300	2.75	34.70	27.69
376	2.81	34.73	400	2.85	34.74	27.71
575	3.11	34.80	(600)	3.15	34.81	27.74

Station 2454; June 4–5; latitude 43°52′ N., longitude 48°50′ W.; depth 1,509 meters; dynamic height 970.923 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	5.36	33.02	0	5.36	33.02	26.09
25	3.19	33.18	25	3.19	33.18	26.44
50	.66	33.65	50	.66	33.65	27.00
67	.46	33.79	75	.65	33.86	27.17
100	1.84	34.12	100	1.84	34.12	27.30
150	2.48	34.35	150	2.48	34.35	27.43
200	2.56	34.54	200	2.56	34.54	27.58
300	2.90	34.71	300	2.90	34.71	27.69
383	2.96	34.76	400	3.00	34.77	27.73
578	3.28	34.85	600	3.30	34.86	27.77
774	3.49	34.90	800	3.50	34.90	27.78
968	3.52	34.915	1,000	3.55	34.92	27.79
1,355	3.52	34.925				

Station 2455; June 5; latitude 43°51′ N., longitude 48°28′ W.; depth 3,191 meters; dynamic height 971.034 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	16.59	35.48	0	16.59	35.48	25.99
25	16.43	35.47	25	16.43	35.47	26.02
51	------	35.01	50	10.70	35.06	26.90
68	2.45	33.62	75	2.85	33.72	26.90
102	4.10	34.22	100	3.95	34.17	27.16
152	4.93	34.44	150	4.90	34.44	27.26
204	3.76	34.33	200	3.80	34.33	27.29
306	4.21	34.60	300	4.15	34.56	27.44
374	6.42	35.10	400	6.30	35.09	27.60
560	4.91	35.03	600	4.75	35.02	27.74
742	4.36	35.01	800	4.20	35.01	27.80
935	3.98	35.00	1,000	3.90	34.99	27.81
1,327	3.56	34.96				

Station 2456; June 5; latitude 43°48′ N., longitude 47°53′ W.; depth 3,878 meters; dynamic height 971.097 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	12.95	33.91	0	12.95	33.91	25.58
22	14.00	35.37	25	13.95	35.37	26.50
44	13.02	35.32	50	12.75	35.28	26.68
58	12.57	35.26	75	12.45	35.31	26.76
88	12.40	35.34	100	12.35	35.38	26.83
132	12.04	35.42	150	11.60	35.32	26.93
176	9.70	35.15	200	9.55	35.21	27.21
264	8.15	35.08	300	7.55	35.03	27.38
220	9.43	35.25	400	6.60	35.07	27.55
322	7.21	35.02	600	5.10	35.06	27.73
418	6.43	35.08	800	4.35	35.01	27.78
538	5.46	35.07	(1,000)	3.95	34.97	27.79
796	4.36	35.01				

Station 2457; June 5; latitude 43°26′ N., longitude 47°08′ W.; depth 3,905 meters; dynamic height 970.987 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	12.30	33.58	0	12.30	33.58	25.46
25	9.06	33.64	25	9.06	33.64	26.06
50	3.53	33.65	50	3.53	33.65	26.78
68	2.94	33.82	75	2.90	33.90	27.04
101	2.91	34.10	100	2.90	34.09	27.19
151	4.31	34.92	150	4.30	34.35	27.38
202	5.43	34.80	200	5.40	34.79	27.48
303	6.45	35.12	300	6.45	35.12	27.61
403	5.51	35.07	400	5.55	35.07	27.64
604	4.66	35.04	600	4.65	35.04	27.77
805	4.14	35.00	800	4.15	35.00	27.79
1,006	3.73	34.96	1,000	3.75	34.96	27.80
1,408	3.42	34.95				

Station 2,458; June 5; latitude 43°14′ N., longitude 47°51′ W.; depth 3,365 meters; dynamic height 970.957 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	12.84	33.66	0	12.84	33.66	25.40
25	10.43	34.32	25	10.43	34.32	26.36
51	3.32	33.85	50	3.35	33.85	26.95
73	3.89	34.20	75	3.90	34.20	27.18
101	2.92	34.18	100	2.95	34.18	27.25
152	4.72	34.63	150	4.65	34.61	27.43
203	5.14	34.81	200	5.15	34.80	27.52
304	4.80	34.92	300	4.80	34.91	27.65
395	5.21	35.04	400	5.20	35.04	27.70
589	4.35	35.00	600	4.30	35.00	27.77
779	4.03	34.98	800	4.00	34.98	27.79
979	3.79	34.97	1,000	3.80	34.97	27.81
1,385	3.32	34.95				

Station 2459; June 6; latitude 43°04′ N., longitude 48°32′ W.; depth, 2,616 meters; dynamic height 970.952 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	12.08	33.72	0	12.08	33.72	25.60
25	6.60	33.55	25	6.60	33.55	26.35
51	5.37	34.22	50	5.40	34.18	27.00
68	8.26	34.84	75	8.20	34.87	27.16
102	7.77	34.90	100	7.80	34.90	27.24
153	6.66	34.92	150	6.75	34.92	27.41
204	4.34	34.70	200	4.40	34.71	27.53
306	4.77	34.92	300	4.75	34.91	27.65
406	4.80	35.00	400	4.85	35.00	27.71
606	4.03	34.96	600	4.05	34.96	27.77
805	3.89	34.96	800	3.90	34.96	27.79
1,009	3.60	34.95	1,000	3.60	34.95	27.81
1,421	3.36	34.93				

Station 2460; June 6; latitude 43°12′ N., longitude 49°05′ W.; depth 1,563 meters; dynamic height 970.906 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	6.86	33.04	0	6.86	33.04	25.91
25	1.70	33.58	25	1.70	33.58	26.88
51	.56	33.82	50	.60	33.81	27.13
68	.86	33.93	75	1.10	33.99	27.25
102	1.83	34.22	100	1.80	34.19	27.36
153	2.08	34.41	150	2.05	34.39	27.50
204	3.46	34.72	200	3.35	34.70	27.63
306	4.93	34.99	300	4.90	34.98	27.69
406	3.51	34.85	400	3.55	34.85	27.73
610	3.45	34.86	600	3.45	34.86	27.75
814	3.62	34.925	800	3.60	34.92	27.79
1,016	3.53	34.92	1,000	3.55	34.92	27.79
1,418	3.45	34.93				

TABLE OF OCEANOGRAPHIC DATA—Continued

STATIONS OCCUPIED IN 1937—Continued

Station 2461; June 6; latitude 43°13′ N., longitude 49°14′ W.; depth, 1,051 meters; dynamic height 970.946 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	6.07	32.98	0	6.07	32.98	25.97
25	.49	33.26	25	.49	33.26	26.69
51	—.68	33.45	50	—.65	33.44	26.90
68	—.58	33.55	75	—.50	33.60	27.02
101	—.17	33.81	100	—.20	33.80	27.17
152	1.64	34.36	150	1.60	34.35	27.50
203	2.07	34.48	200	2.05	34.47	27.57
304	2.67	34.64	300	2.65	34.63	27.64
398	3.38	34.80	400	3.40	34.80	27.71
599	3.42	34.84	600	3.45	34.84	27.73
800	3.53	34.90	800	3.55	34.90	27.77
1,000	3.55	34.90	1,000	3.55	34.90	27.77

Station 2462; June 6; latitude 43°14′ N., longitude 49°19′ W.; depth 640 meters; dynamic height 970.983 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	5.35	33.02	0	5.35	33.02	26.09
25	—.79	33.28	25	—.79	33.28	26.77
51	—1.01	33.40	50	—1.00	33.40	26.88
67	—.88	33.52	75	—.80	33.56	27.00
102	—.58	33.66	100	—.60	33.65	27.06
153	.08	33.88	150	.00	33.86	27.21
203	.89	34.12	200	.80	34.10	27.35
305	2.34	34.51	300	2.30	34.49	27.56
407	2.84	34.70	400	2.85	34.69	27.69
603	3.34	34.84	600	3.35	34.84	27.74

Station 2463; June 6; latitude 43°18′ N., longitude 49°33′ W.; depth 220 meters; dynamic height 971.027 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	6.81	33.13	0	6.81	33.13	25.99
25	.74	33.30	25	.74	33.30	26.71
51	—.32	33.44	50	—.30	33.44	26.88
76	—.48	33.52	75	—.50	33.52	26.96
101	—.47	33.59	100	—.45	33.58	27.00
152	—.07	33.76	150	—.10	33.74	27.11
203	.82	34.04	200	.75	34.02	27.30

Station 2464; June 6; latitude 43°19′ N., longitude 49°41′ W.; depth 62 meters; dynamic height 971.039 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	7.38	33.12	0	7.38	33.12	25.90
26	2.92	33.18	25	3.10	33.18	26.45
53	.47	33.33	50	.65	33.30	26.72

Station 2465; June 6; latitude 43°25′ N., longitude 50°09′ W.; depth 60 meters; dynamic height 971.065 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	9.56	32.53	0	9.56	32.53	25.12
25	5.11	32.88	25	5.11	32.88	26.01
51	1.57	33.08	50	1.65	33.08	26.48

Station 2466; June 21; latitude 41°44′ N., longitude 50°41′ W.; depth 3,604 meters; dynamic height 1,937.572 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	12.03	33.21	0	12.03	33.21	25.21
24	11.71	34.20	25	11.70	34.20	26.04
49	6.03	33.72	50	5.60	33.70	26.60
64	1.35	33.40	75	.40	33.43	26.84
98	—.75	33.51	100	—.75	33.54	26.98
147	1.52	33.86	150	1.55	33.87	27.12
195	1.88	33.96	200	2.10	33.98	27.16
293	.82	34.04	300	1.05	34.05	27.30
268	5.07	34.44	400	4.65	34.76	27.55
394	4.53	34.74	600	4.65	34.98	27.72
514	5.11	34.99	800	4.30	34.97	27.75
629	4.59	34.98	1,000	4.05	34.96	27.77
990	4.05	34.97	1,500	3.55	34.94	27.80
1,385	3.63	34.945	2,000	3.35	34.94	27.82
1,805	3.41	34.935	2,500	3.10	34.93	27.84
2,250	3.32	34.94	(3,000)	2.75	34.91	27.86
2,628	2.98	34.92				

Station 2467; June 21; latitude 42°11′ N., longitude 50°33′ W.; depth 3,158 meters; dynamic height 1,937.492 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	13.74	33.88	0	13.74	33.88	25.40
23	11.07	34.33	25	10.80	34.33	26.30
45	6.97	34.04	50	7.05	34.08	26.70
59	7.31	34.33	75	8.30	34.71	27.02
90	9.30	34.95	100	8.95	34.91	27.08
135	7.46	34.78	150	7.00	34.75	27.24
180	6.22	34.68	200	5.50	34.61	27.33
270	4.35	34.64	300	4.25	34.69	27.53
225	4.32	34.50	400	3.65	34.78	27.66
347	3.93	34.74	600	3.50	34.85	27.74
476	3.47	34.81	800	3.60	34.88	27.75
612	3.52	34.85	1,000	3.60	34.90	27.77
993	3.62	34.90	1,500	3.50	34.93	27.80
1,425	3.56	34.93	2,000	3.30	34.92	27.82
2,223	3.25	34.92	2,500	3.00	34.92	27.85
2,472	3.03	-------	(3,000)	2.40	34.92	27.90
2,697	2.77	34.92				

Station 2468; June 21; latitude 42°38′ N., longitude 50°24′ W.; depth 1,988 meters; dynamic height 1,937.467 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	8.14	32.83	0	8.14	32.83	25.58
25	1.16	33.21	25	1.16	33.21	26.63
50	—.20	33.48	50	—.20	33.48	26.91
64	—.04	33.71	75	.10	33.82	27.17
101	.59	34.03	100	.55	34.02	27.31
151	1.31	34.24	150	1.30	34.24	27.43
201	1.75	34.38	200	1.75	34.37	27.50
302	2.53	34.58	300	2.55	34.57	27.61
379	2.61	34.63	400	2.65	34.66	27.67
571	2.99	34.72	600	3.05	34.74	27.69
763	3.37	34.84	800	3.40	34.84	27.74
957	3.48	34.86	1,000	3.50	34.86	27.75
1,449	3.69	34.915	1,500	3.65	34.91	27.77
1,848	3.48	34.91				

TABLE OF OCEANOGRAPHIC DATA—Continued

STATIONS OCCUPIED IN 1937—Continued

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
Station 2469; June 22; latitude 42°48′ N., longitude 50°19′ W.; depth 625 meters; dynamic height 1,937.541 meters						
0	7.89	32.85	0	7.89	32.85	25.62
26	7.58	32.89	25	7.60	32.89	25.69
51	−.55	33.42	50	−.40	33.39	26.85
66	−.76	33.45	75	−.75	33.50	26.95
102	−.57	33.65	100	−.60	33.64	27.05
153	.22	33.91	150	.20	33.90	27.23
205	.99	34.15	200	.95	34.13	27.36
307	1.68	34.34	300	1.65	34.33	27.48
404	2.70	34.62	400	2.65	34.61	27.63
608	3.23	34.79	600	3.20	34.79	27.72
Station 2470; June 22; latitude 43°00′ N., longitude 50°13′ W.; depth 90 meters; dynamic height 1,937.537 meters						
0	10.84	32.81	0	10.84	32.81	25.12
26	1.88	33.26	25	2.00	33.25	26.60
51	−.05	33.43	50	0.00	33.43	26.86
77	−.20	33.46	75	−.20	33.46	26.90
Station 2471; June 22; latitude 43° 19′ N., longitude 50°06′ W.; depth 64 meters; dynamic height 1,937.549 meters						
0	11.18	32.48	0	11.18	32.48	24.80
26	1.66	33.10	25	1.70	33.08	26.48
50	.45	33.24	50	.46	33.24	26.69
Station 2472; June 22; latitude 43°05′ N., longitude 49°49′ W.; depth 92 meters; dynamic height 1,937.535 meters						
0	10.30	32.79	0	10.30	32.79	25.20
26	.23	33.26	25	.40	33.25	26.70
52	−.58	33.44	50	−.55	33.42	26.88
78	−.72	33.58	75	−.75	33.56	27.00
Station 2473; June 22; latitude 43°00′ N., longitude 49°43′ W.; depth 230 meters; dynamic height 1,937.524 meters						
0	9.18	32.88	0	9.18	32.88	25.45
25	−.36	33.33	25	−.36	33.33	26.79
51	−.82	33.46	50	−.80	33.45	26.91
76	−.69	33.61	75	−.70	33.61	27.04
102	−.29	33.78	100	−.35	33.76	27.14
153	.19	33.92	150	.15	33.91	27.24
204	.78	34.07	200	.70	34.06	27.33
Station 2474; June 22; latitude 42°50′ N., longitude 49°31′ W.; depth 1,725 meters: dynamic height 1,937.470 meters						
0	7.99	32.84	0	7.99	32.84	25.61
25	4.22	33.13	25	4.22	33.13	26.30
51	3.54	33.62	50	3.60	33.58	26.73
66	2.28	33.70	75	2.00	33.78	27.01
102	1.68	34.18	100	1.65	34.15	27.34
153	1.74	34.32	150	1.75	34.31	27.46
203	2.12	34.45	200	2.10	34.44	27.53
305	2.51	34.57	300	2.50	34.56	27.60
399	3.53	34.77	400	3.55	34.77	27.67
599	3.31	34.79	600	3.35	34.79	27.70
799	3.53	34.85	800	3.55	34.85	27.73
999	3.58	34.89	1,000	3.60	34.89	27.76
1,365	3.45	34.885	1,500	3.40	34.89	27.78
1,602	3.40	34.89				
Station 2475; June 22: latitude 42°45′ N., longitude 49°17′ W.; depth 2,234 meters; dynamic height 1,937.426 meters						
0	7.98	32.93	0	7.98	32.93	25.67
25	2.38	33.62	25	2.38	33.62	26.86
51	1.48	33.85	50	1.50	33.84	27.10
66	1.87	33.95	75	2.40	34.05	27.20
101	3.83	34.40	100	3.80	34.39	27.34
152	3.93	34.54	150	3.90	34.52	27.44
203	5.16	34.80	200	5.15	34.79	27.51
304	4.72	34.89	300	4.80	34.89	27.63
406	3.60	34.81	400	3.65	34.91	27.69
608	3.37	34.82	600	3.35	34.82	27.72
810	3.47	34.85	800	3.45	34.85	27.74
1,011	3.69	34.90	1,000	3.70	34.89	27.75
1,516	3.39	34.91	1,500	3.40	34.91	27.80
1,935	3.27	34.89	2,000	3.20	34.89	27.80
2,181	3.17					
Station 2476; June 22; latitude 42°35′ N., longitude 49°04′ W.; depth 2,633 meters; dynamic height 1,937.439 meters						
0	14.47	33.49	0	14.47	33.49	24.94
25	6.30	33.60	25	6.30	33.60	26.43
50	1.39	33.77	50	1.40	33.77	27.05
66	1.01	33.90	75	1.15	33.97	27.23
101	1.71	34.17	100	1.70	34.15	27.33
151	2.65	34.45	150	2.60	34.45	27.50
201	3.61	34.70	200	3.60	34.70	27.61
302	4.21	34.86	300	4.20	34.86	27.68
406	4.44	34.93	400	4.45	34.93	27.70
608	4.06	34.925	600	4.05	34.93	27.74
810	3.76	34.90	800	3.80	34.90	27.75
1,011	3.52	34.90	1,000	3.55	34.90	27.77
1,279	3.43	34.90	1,500	3.35	34.88	27.77
1,514	3.38	34.88	2,000	3.20	34.86	27.78
2,017	3.22	34.86	2,500	2.95	34.90	27.83
2,282	3.12	34.905				
2,514	2.93	34.90				
Station 2477; June 22; latitude 42°14′ N., longitude 48°35′ W.; depth 3,230 meters, dynamic height 1,937.493 meters						
0	13.63	33.42	0	13.63	33.42	25.07
25	12.29	33.42	25	12.29	33.42	25.33
50	3.43	33.57	50	3.43	33.57	26.73
67	1.69	33.70	75	1.60	33.78	27.04
101	1.48	33.98	100	1.50	33.97	27.21
151	2.32	34.29	150	2.30	34.28	27.39
202	2.55	34.49	200	2.55	34.48	27.53
303	3.21	34.69	300	3.20	34.68	27.63
378	3.87	34.78	400	4.00	34.80	27.65
560	4.57	34.965	600	4.50	34.96	27.72
737	4.13	34.95	800	3.95	34.94	27.76
909	3.72	34.91	1,000	3.60	34.90	27.77
1,386	3.42	34.90	1,500	3.40	34.90	27.79
1,877	3.28	34.89	2,000	3.20	34.89	27.80
2,440	3.04	34.90	2,500	3.00	34.90	27.83
2,891	2.73	34.905	3,000	2.65	34.90	27.86
3,121	2.51	34.895				

TABLE OF OCEANOGRAPHIC DATA—Continued

STATIONS OCCUPIED IN 1937—Continued

Station 2478; June 23; latitude 41°53′ N., longitude 48°08′ W.; depth 3,960 meters; dynamic height 1,937.578 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	12.33	33.16	0	12.33	33.16	25.12
25	9.63	33.17	25	9.63	33.17	25.61
51	2.45	33.29	50	2.60	33.28	26.57
65	.50	33.40	75	.90	33.52	26.89
102	2.92	34.00	100	2.65	33.93	27.08
153	7.17	34.96	150	6.85	34.72	27.24
204	8.69	35.12	200	8.65	35.11	27.28
306	2.65	34.30	300	2.70	34.31	27.38
378	3.44	34.57	400	3.65	34.63	27.54
567	4.43	34.90	600	4.40	34.92	27.70
755	4.24	34.94	800	4.15	34.94	27.74
944	3.90	34.92	1,000	3.80	34.92	27.77
1,426	3.47	34.89	1,500	3.40	34.89	27.78
1,916	3.31	34.90	2,000	3.30	34.90	27.80
2,348	3.13	34.90	2,500	3.05	34.90	27.82
2,829	2.83	34.91	3,000	2.75	34.90	27.85
3,426	2.42	34.90	3,500	2.35	34.90	27.88
3,657	2.27	34.86				

Station 2479; June 23; latitude 41°28′ N.; longitude 47°30′ W.; depth 4,263 meters; dynamic height 1,937.742 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	19.43	35.30	0	19.42	35.30	25.16
25	18.97	35.29	25	18.97	35.29	25.27
50	15.76	35.61	50	15.77	35.61	26.29
64	15.53	35.68	75	15.20	35.66	26.45
99	14.11	35.53	100	14.05	35.51	26.59
149	11.76	35.16	150	11.75	35.16	26.78
198	12.01	35.46	200	12.00	35.46	26.97
297	10.11	35.31	300	10.00	35.29	27.19
395	*2.90	34.25	400	2.90	34.26	27.33
593	3.61	34.71	600	3.65	34.72	27.62
791	4.74	35.00	800	4.75	35.00	27.72
989	4.24	34.97	1,000	4.20	34.97	27.77
1,485	3.58	34.92	1,500	3.55	34.92	27.79
1,983	3.36	34.90	2,000	3.35	34.90	27.79
2,314	3.28	34.915	2,500	3.15	34.92	27.83
2,808	2.97	34.92	3,000	2.80	34.91	27.85
3,311	2.61	34.905	3,500	2.50	34.90	27.87
3,824	2.37	34.895	(4,000)	2.30	34.91	27.90
4,065	2.30	34.91				

Station 2480; June 23; latitude 41°11′ N.; longitude 47°03′ W.; depth 4,478 meters; dynamic height 1,938.053 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	23.07	36.18	0	23.07	36.18	24.83
25	------	36.26	25	22.10	36.36	25.16
50	------	36.56	50	21.00	36.56	25.70
66	20.30	36.54	75	19.90	36.53	25.97
101	18.84	36.48	100	18.90	36.48	26.20
151	17.47	36.26	150	17.50	36.26	26.37
202	17.67	36.42	200	17.65	36.42	26.46
303	15.91	36.13	300	16.05	36.15	26.63
366	13.37	35.73	400	12.25	35.53	26.97
527	8.91	35.04	600	7.20	34.95	27.37
673	5.81	34.92	800	4.90	34.98	27.69
804	4.87	34.98	1,000	4.50	34.97	27.73
1,281	4.15	34.95	1,500	3.90	34.94	27.77
1,808	3.53	34.93	2,000	3.40	34.93	27.81
1,948	3.40	-------	2,500	3.25	34.92	27.82
2,378	3.31	34.92	3,000	3.05	34.92	27.84
2,820	3.13	34.92	3,500	2.70	34.92	27.87
3,272	2.86	34.92	(4,000)	2.30	34.90	27.89
3,513	2.69	34.92				
3,733	2.50	34.905				

Station 2481; June 24; latitude 40°54′ N., longitude 46°36′ W.; depth 4,553 meters; dynamic height 1,938.203 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	21.70	36.33	0	21.70	36.33	25.33
25	21.31	36.32	25	21.31	36.32	25.43
50	17.83	36.30	50	17.84	36.30	26.32
65	17.50	36.30	75	17.45	36.31	26.41
101	17.34	36.34	100	17.35	36.34	26.48
151	17.03	36.30	150	17.05	36.30	26.52
201	16.66	36.24	200	16.65	36.24	26.56
302	16.25	36.22	300	16.25	36.22	26.64
400	*16.11	36.20	400	16.10	36.20	26.67
601	12.17	35.55	600	12.20	35.55	27.00
803	7.34	35.02	800	7.40	35.02	27.40
1,005	5.22	34.98	1,000	5.25	34.98	27.65
1,503	4.08	34.965	1,500	4.10	34.96	27.77
2,000	3.51	34.935	2,000	3.50	34.94	27.81

Station 2482; June 24; latitude 40°38′ N., longitude 46°10′ W.; depth 4,535 meters; dynamic height 1,938.201 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	21.94	36.32	0	21.94	36.32	25.25
25	20.20	-------	25	20.20	36.33	25.74
50	18.25	36.35	50	18.25	36.35	26.26
64	18.09	36.42	75	18.00	36.42	26.38
100	17.86	36.42	100	17.86	36.42	26.41
150	17.57	36.40	150	17.54	36.40	26.47
201	16.88	36.28	200	16.90	36.28	26.54
301	16.36	36.23	300	16.35	36.23	26.62
403	16.15	36.22	400	16.15	36.22	26.67
604	11.98	35.53	600	12.10	35.55	27.02
804	7.22	35.03	800	7.30	35.05	27.42
1,004	5.50	35.07	1,000	5.50	35.07	27.69
1,501	3.86	34.94	1,500	3.85	34.94	27.77
1,998	3.47	34.93	2,000	3.45	34.93	27.80
2,442	3.33	34.93	2,500	3.30	34.93	27.82
2,941	3.06	34.935	3,000	3.00	34.93	27.85
3,440	2.68	34.92	3,500	2.65	34.92	27.88
3,942	2.42	34.91	4,000	2.40	34.91	27.89
4,207	2.36	34.90	(4.500)	2.30	34.90	27.89
4,442	2.31	34.90				

Station 2483; June 24; latitude 40°20′ N., longitude 45°45′ W.; depth 4,549 meters; dynamic height 1,938.227 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	22.18	36.24	0	22.18	36.24	25.13
25	------	36.24	25	20.85	36.24	25.49
50	19.33	36.34	50	19.33	36.34	25.98
65	18.63	36.36	75	18.30	36.36	26.26
101	17.73	36.37	100	17.75	36.37	26.40
151	17.56	36.38	150	17.55	36.38	26.46
201	17.14	36.32	200	17.15	36.32	26.51
302	16.37	36.20	300	16.40	36.20	26.60
411	16.22	36.22	400	16.25	36.22	26.64
604	12.45	35.58	600	12.60	35.60	26.95
788	7.05	35.02	800	6.85	35.02	27.48
964	5.15	34.98	1,000	4.95	34.98	27.68
1,454	3.78	34.93	1,500	3.75	34.93	27.77
1,949	3.50	34.92	2,000	3.50	34.92	27.80

TABLE OF OCEANOGRAPHIC DATA—Continued

STATIONS OCCUPIED IN 1937—Continued

Station 2484; June 24–25; latitude 40°00′ N., longitude 45°16′ W.; depth 4,530 meters; dynamic height 1,938.192 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	22.72	36.25	0	22.72	36.25	24.98
24	21.71	36.30	25	21.70	36.30	25.30
48	20.80	36.35	50	20.60	36.35	25.67
62	19.31	36.35	75	18.60	36.34	26.16
96	17.99	36.31	100	17.95	36.31	26.30
144	17.69	36.38	150	17.65	36.38	26.43
192	17.24	36.32	200	17.15	36.31	26.50
288	16.46	36.22	300	16.40	36.22	26.61
392	16.16	36.22	400	16.15	36.21	26.66
590	11.14	35.40	600	10.85	35.36	27.10
791	6.50	35.00	800	6.40	35.00	27.52
993	5.05	35.01	1,000	5.00	35.01	27.71
1,485	3.85	34.94	1,500	3.85	34.94	27.77
1,976	3.42	34.92	2,000	3.40	34.92	27.81
2,336	3.28	34.905	2,500	3.20	34.91	27.82
2,823	3.09	34.92	3,000	2.95	34.92	27.85
3,312	2.74	34.915	3,500	2.65	34.91	27.87
3,804	2.44	34.90	4,000	2.40	34.89	27.87
4,067	2.36	34.89	(4,500)	2.30	34.88	27.87
4,299	2.30	34.88				

Station 2485; June 25; latitude 40°42′ N., longitude 44°21′ W.; depth 4,852 meters; dynamic height 1,937.695 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	21.74	35.24	0	21.74	35.24	24.48
25	17.33	35.14	25	17.33	35.14	25.56
50	13.45	35.28	50	13.45	35.28	26.54
66	13.22	35.29	75	12.95	35.26	26.63
99	11.91	35.08	100	11.90	35.08	26.69
149	11.89	35.34	150	11.90	35.34	26.89
199	10.67	35.28	200	10.65	35.28	27.07
298	8.13	35.02	300	8.05	35.01	27.30
378	7.00	34.97	400	6.75	34.97	27.45
568	5.39	34.96	600	5.20	34.96	27.64
757	4.60	34.98	800	4.50	34.98	27.73
947	4.26	34.965	1,000	4.20	34.96	27.76
1,432	3.64	34.93	1,500	3.60	34.93	27.79
1,923	3.38	34.90	2,000	3.35	34.90	27.79

Station 2486; June 25; latitude 41°52′ N., longitude 43°44′ W.; depth 4,927 meters; dynamic height 1,938.456 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	22.72	36.00	0	22.72	36.00	24.80
24	22.51	35.99	25	22.50	35.99	24.84
49	20.60	36.53	50	20.55	36.53	25.80
64	19.42	36.41	75	19.10	36.42	26.10
98	18.68	36.46	100	18.60	36.46	26.26
147	18.08	36.42	150	18.05	36.42	26.36
195	17.89	36.40	200	17.90	36.40	26.39
293	17.86	36.40	300	17.85	36.40	26.40
363	17.39	36.36	400	17.10	36.32	26.52
713	11.74	35.48	600	14.20	35.88	26.84
883	7.85	35.09	800	9.75	35.22	27.18
1,323	4.51	34.98	1,000	6.40	35.04	27.55
1,759	3.79	34.95	1,500	4.05	34.97	27.78
479	16.30	36.19	2,000	3.60	34.92	27.79
1,872	3.64	34.92	2,500	3.35	34.92	27.81
2,289	3.43	34.92	3,000	3.05	34.92	27.84
2,719	3.24	34.93	3,500	2.70	34.92	27.87
3,160	2.97	34.92	(4,000)	2.40	34.91	27.89
3,402	2.79	34.92				
3,619	2.62	34.91				

Station 2487; June 26; latitude 42°52′ N., longitude 43°04′ W.; depth 4,913 meters; dynamic height 1,938.246 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	21.85	36.25	0	21.85	36.25	25.22
23	21.85	36.25	25	21.85	36.25	25.22
45	21.04	36.41	50	20.85	36.41	25.62
59	20.36	36.42	75	19.60	36.44	25.98
90	18.92	36.45	100	18.60	36.45	26.25
135	18.01	36.42	150	17.95	36.41	26.38
181	17.76	36.40	200	17.60	36.38	26.44
271	16.87	36.27	300	16.70	36.25	26.56
383	16.21	36.22	400	16.00	36.20	26.69
592	11.96	35.52	600	11.80	35.49	27.02
814	6.73	34.99	800	6.90	35.00	27.45
1,049	5.16	35.03	1,000	5.40	35.03	27.67
1,590	3.85	34.95	1,500	3.95	34.96	27.78
2,142	3.46	34.925	2,000	3.55	34.93	27.79

Station 2488; June 26; latitude 43°47′ N., longitude 42°06′ W.; depth 4,791 meters; dynamic height 1,937.611 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	20.00	34.75	0	20.00	34.75	24.59
25	15.97	34.68	25	15.97	34.68	25.52
49	10.04	34.54	50	10.05	34.54	26.60
64	10.40	34.76	75	10.40	34.82	26.76
99	10.26	34.88	100	10.25	34.88	26.83
148	7.31	34.54	150	7.30	34.55	27.04
197	7.11	34.69	200	7.10	34.70	27.19
296	6.46	34.78	300	6.45	34.78	27.34
353	6.00	34.88	400	5.80	34.91	27.53
535	5.14	34.96	600	4.90	34.97	27.69
720	4.55	34.98	800	4.35	34.97	27.75
909	4.00	34.96	1,000	3.80	34.95	27.79
1,383	3.54	34.92	1,500	3.50	34.92	27.80
1,872	3.35	34.91	2,000	3.30	34.81	27.81
2,286	3.24	34.92	2,500	3.15	34.93	27.83
2,767	2.99	34.935	3,000	2.85	34.93	27.86
3,253	2.67	34.92	3,500	2.55	34.91	27.88
3,745	2.44	34.905	4,000	2.40	34.895	27.88
4,008	2.38	34.89	(4,500)	2.35	34.895	27.88
4,243	2.35	34.89				

Station 2489; June 26–27; latitude 43°53′ N., longitude 42°46′ W.; depth 4,814 meters; dynamic height 1,937.856 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	19.65	35.71	0	19.65	35.71	25.42
25	16.65	35.75	25	16.65	35.75	26.19
50	14.43	35.60	50	14.43	35.60	26.57
65	14.03	35.65	75	13.95	35.57	26.66
99	13.88	35.61	100	13.90	35.61	26.70
149	14.30	35.84	150	14.30	35.84	26.79
198	13.23	35.67	200	13.20	35.67	26.89
297	12.26	35.58	300	12.25	35.57	27.00
368	11.79	35.54	400	11.50	35.49	27.08
552	8.24	35.08	600	7.45	35.04	27.40
736	5.84	35.00	800	5.55	35.01	27.64
920	5.19	35.06	1,000	4.95	35.05	27.745
1,395	3.85	34.96	1,500	3.75	34.95	27.79
1,882	3.49	34.92	(2,000)	3.40	34.92	27.81

TABLE OF OCEANOGRAPHIC DATA—Continued

STATIONS OCCUPIED IN 1937—Continued

Station 2490; June 27; latitude 44°00′ N., longitude 43°27′ W.; depth 4,805 meters; dynamic height 1,937.899 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	20.76	35.40	0	20.76	35.40	24.88
25	16.70	35.76	25	16.70	35.76	26.19
50	15.96	35.92	50	15.96	35.92	26.48
63	15.70	35.94	75	15.50	35.93	26.60
100	14.98	35.88	100	14.98	35.88	26.66
150	14.66	35.92	150	14.66	35.92	26.78
200	13.33	35.70	200	13.33	35.70	26.88
300	12.45	35.62	300	12.45	35.62	27.00
402	12.15	35.60	400	12.20	35.60	27.03
602	8.38	35.10	600	8.45	35.10	27.30
802	5.83	35.05	800	5.85	35.05	27.63
1,001	5.01	35.05	1,000	5.00	35.05	27.74
1,500	3.76	34.96	1,500	3.76	34.96	27.80
2,000	3.43	34.93	2,000	3.42	34.93	27.81
2,446	3.24	34.91	2,500	3.20	34.91	27.82
2,944	3.02	34.93	3,000	3.00	34.93	27.85
3,443	2.69	34.93	3,500	2.65	34.93	27.88
3,938	2.47	34.915	4,000	2.45	34.91	27.88
4,203	2.40	34.90	(4,500)	2.35	34.91	27.89
4,435	2.36	34.91				

Station 2491; June 27; latitude 44°03′ N., longitude 44°13′ W.; depth 4,824 meters; dynamic height 1,937.878 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	20.31	35.66	0	20.31	35.66	25.20
25	16.33	35.60	25	16.33	35.60	26.15
50	14.36	35.60	50	14.36	35.60	26.59
66	13.90	35.57	75	13.95	35.60	26.68
100	14.09	35.71	100	14.09	35.71	26.73
150	13.70	35.72	150	13.70	35.72	26.82
199	13.23	35.71	200	13.25	35.71	26.91
299	12.40	35.63	300	12.40	35.63	27.01
395	11.85	35.55	400	11.80	35.54	27.06
591	7.83	35.00	600	7.70	35.00	27.34
785	5.85	35.02	800	5.75	35.02	27.62
978	4.94	35.03	1,000	4.90	35.03	27.73
1,470	3.82	34.955	1,500	3.80	34.95	27.79
1,965	3.44	34.93	2,000	3.40	34.93	27.81

Station 2492; June 27; latitude 44°09′ N., longitude 44°51′ W.; depth 4,431 meters; dynamic height 1,937.815 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	22.08	35.61	0	22.08	35.61	24.68
25	16.71	35.53	25	16.71	35.53	26.01
50	16.27	36.01	50	16.27	36.01	26.48
65	15.69	35.92	75	15.25	35.85	26.59
100	14.45	35.68	100	14.45	35.68	26.63
150	14.06	35.69	150	14.06	35.69	26.72
201	13.17	35.58	200	13.20	35.58	26.82
301	11.77	35.51	300	11.80	35.51	27.04
398	9.45	35.18	400	9.40	35.17	27.21
598	6.45	35.01	600	6.45	35.01	27.52
798	5.04	34.99	800	5.05	34.99	27.68
998	4.39	34.99	1,000	4.40	34.99	27.75
1,496	3.60	34.93	1,500	3.60	34.93	27.79
1,993	3.37	34.93	2,000	3.35	34.93	27.81
2,486	3.17	34.94	2,500	3.15	34.94	27.84
2,982	2.84	34.92	3,000	2.85	34.92	27.86
3,479	2.49	34.90	3,500	2.50	34.90	27.87
4,042	2.34	34.91	4,000	2.35	34.91	27.89
4,276	2.22	34.905				

Station 2493; June 27–28; latitude 44°18′ N., longitude 45°33′ W.; depth 4,188 meters; dynamic height 1,937.739 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	21.83	35.75	0	21.83	35.75	24.85
25	18.53	35.60	25	18.53	35.60	25.62
50	14.27	35.34	50	14.27	35.34	26.40
64	13.77	35.34	75	13.65	35.35	26.55
100	13.50	35.41	100	13.51	35.41	26.63
150	12.27	35.25	150	12.27	35.25	26.76
201	12.08	35.40	200	12.10	35.40	26.90
301	9.82	35.22	300	9.85	35.22	27.17
401	7.76	35.04	400	7.80	35.04	27.35
602	4.51	34.82	600	4.55	34.82	27.61
803	4.14	34.90	800	4.15	34.90	27.71
1,005	3.82	34.92	1,000	3.85	34.92	27.76
1,503	3.47	34.905	1,500	3.45	34.91	27.79
1,998	3.29	34.915	2,000	3.25	34.91	27.81
2,509	3.11	34.915	2,500	3.10	34.91	27.83
3,009	2.83	34.90	3,000	2.85	34.90	27.84
3,510	2.50	34.91	3,500	2.50	34.91	27.88
3,931	2.31	34.91	4,000	2.30	34.90	27.89
4,167	2.18	34.895				

Station 2494; June 28; latitude 44°25′ N., longitude 46°13′ W.; depth 3,794 meters; dynamic height 1,937.702 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	20.95	35.56	0	20.95	35.56	24.95
25	18.14	35.44	25	18.14	35.44	25.59
50	13.97	35.26	50	13.97	35.26	26.41
66	13.70	35.34	75	13.65	35.39	26.58
100	13.62	35.49	100	13.62	35.49	26.66
150	12.40	35.34	150	12.40	35.34	26.79
201	11.64	35.39	200	11.65	35.39	26.97
301	8.93	35.11	300	8.90	35.11	27.24
404	7.10	34.98	400	7.20	34.99	27.40
604	4.83	34.92	600	4.85	34.92	27.65
803	4.22	34.93	800	4.25	34.93	27.72
1,001	3.75	34.915	1,000	3.75	34.92	27.77
1,502	3.38	34.90	1,500	3.40	34.90	27.79
2,003	3.26	34.905	2,000	3.25	34.91	27.81
2,499	3.06	34.925	2,500	3.05	34.92	27.84
2,997	2.71	34.90	3,000	2.70	34.90	27.85
3,523	2.33	34.90	3,500	2.35	34.90	27.88
3,763	2.18	34.91				

Station 2495; June 28; latitude 44°32′ N.; longitude 46°54′ W.; depth 3,709 meters; dynamic height 1,937.674 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	20.78	35.64	0	20.78	35.64	25.06
25	16.07	35.54	25	16.07	35.54	26.16
50	14.58	35.56	50	14.58	35.56	26.51
67	14.20	35.52	75	13.95	35.48	26.58
101	13.10	35.36	100	13.15	35.37	26.67
151	12.75	35.45	150	12.75	35.45	26.81
202	11.54	35.37	200	11.65	35.38	26.97
303	9.14	35.18	300	9.20	35.19	27.25
407	7.72	35.11	400	7.85	35.11	27.40
607	4.68	34.92	600	4.70	34.92	27.67
806	4.44	34.97	800	4.45	34.97	27.74
1,001	4.12	34.98	1,000	4.15	34.98	27.77
1,500	3.39	34.91	1,500	3.39	34.91	27.80
1,998	3.25	34.91	2,000	3.25	34.91	27.81
2,605	2.93	34.92	2,500	3.00	34.92	27.85
3,003	2.67	34.91	3,000	2.65	34.91	27.87
3,455	2.31	34.89	3,500	2.30	34.89	27.88
3,689	2.19	34.895				

TABLE OF OCEANOGRAPHIC DATA—Continued

STATIONS OCCUPIED IN 1937—Continued

Station 2496; June 28; latitude 44°38′ N., longitude 47°35′ W.; depth 3,661 meters; dynamic height 1,937.460 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	17.47	33.63	0	17.47	33.63	24.38
25	7.40	33.50	25	7.40	33.50	26.20
51	5.09	33.82	50	5.20	33.81	26.74
65	4.23	33.96	75	4.25	34.06	27.04
101	4.53	34.26	100	4.55	34.25	27.15
152	2.46	34.16	150	2.50	34.16	27.28
203	3.98	34.51	200	3.95	34.49	27.40
304	3.96	34.74	300	3.95	34.73	27.59
389	4.25	34.87	400	4.25	34.88	27.68
581	3.93	34.91	600	3.90	34.91	27.75
772	3.81	34.92	800	3.80	34.92	27.77
962	3.62	34.92	1,000	3.60	34.92	27.79
1,448	3.32	34.905	1,500	3.30	34.91	27.81
1,935	3.17	34.925	2,000	3.10	34.93	27.84
2,382	2.84	34.93	2,500	2.80	24.93	27.86
2,966	2.55	34.92	3,000	2.55	34.92	27.89
3,348	2.32	34.905	3,500	2.25	34.90	27.89
3,575	2.19	34.90				

Station 2497; June 29; latitude 44°45′ N., longitude 48°16′ W.; depth 2,936 meters; dynamic height 1,937.387 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	14.52	33.03	0	14.52	33.03	24.57
25	4.28	33.90	25	4.28	33.90	26.90
50	2.07	33.98	50	2.07	33.98	27.17
62	2.20	34.08	75	2.15	34.15	27.30
101	1.96	34.24	100	1.95	34.23	27.38
151	4.64	34.75	150	4.60	34.73	27.52
201	5.10	34.90	200	5.10	34.90	27.60
302	4.66	34.94	300	4.65	34.94	27.69
398	4.22	34.92	400	4.20	34.92	27.73
596	3.84	34.91	600	3.85	34.91	27.75
793	3.62	34.90	800	3.65	34.90	27.76
991	3.59	34.92	1,000	3.60	34.92	27.79
1,487	3.33	34.90	1,500	3.30	34.90	27.80
2,006	3.20	34.91	2,000	3.20	34.91	27.82
2,505	2.96	34.91	2,500	2.95	34.91	27.84
2,671	2.91	34.91	(3,000)	2.70	34.91	27.86
2,904	2.74	34.91				

Station 2498; June 29; latitude 44°50′ N., longitude 48°44′ W.; depth 1,379 meters; dynamic height 1,937.367 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	13.88	32.92	0	13.88	32.92	24.62
25	4.38	33.71	25	4.38	33.71	26.75
51	2.76	34.14	50	2.80	34.13	27.23
66	2.63	34.25	75	2.65	34.31	27.40
102	2.64	34.45	100	2.65	34.44	27.49
153	2.64	34.57	150	2.65	34.57	27.60
203	2.88	34.67	200	2.85	34.66	27.65
305	3.32	34.78	300	3.30	34.78	27.70
398	3.45	34.83	400	3.45	34.83	27.72
597	3.47	34.86	600	3.45	34.86	27.75
796	3.40	34.89	800	3.40	34.89	27.78
1,060	3.40	34.89	1,000	3.40	34.89	27.78
1,292	3.31	34.895				

Station 2499; June 29; latitude 44°52′ N., longitude 48°59′ W.; depth 579 to 430 meters; dynamic height 1,937.444 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	10.26	32.13	0	10.26	32.13	24.70
25	−1.41	33.16	25	−1.41	33.16	26.69
49	−1.19	33.36	50	−1.15	33.37	26.86
72	−.90	33.56	75	−.90	33.58	27.02
99	−.02	33.86	100	0.00	33.88	27.22
148	.80	34.11	150	.90	34.13	27.37
197	1.87	34.39	200	1.95	34.40	27.52
296	2.72	34.62	300	2.70	34.62	27.63
360	2.81	34.64	(400)	2.85	34.65	27.64

Station 2500; June 29; latitude 44°53′ N., longitude 49°03′ W.; depth 175 to 91 meters; dynamic height 1,937.479 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	8.47	32.24	0	8.47	32.24	25.06
28	−1.37	33.17	25	−1.05	33.13	26.66
56	−1.15	33.33	50	−1.20	33.30	26.80
112	−.60	33.58	75	−1.00	33.42	26.90
			100	−.75	33.52	26.97
			(150)	−.20	33.79	27.16

Station 2501; June 29; latitude 44°54′ N., longitude 49°10′ W.; depth 68 meters; dynamic height 1,937.493 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	12.44	32.03	0	12.44	32.03	24.23
27	−.52	33.10	25	−.10	33.06	26.56
54	−.98	33.37	50	−.95	33.34	26.83

Station 2502; June 29; latitude 44°57′ N., longitude 49°29′ W.; depth 66 meters; dynamic height 1,937.491 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	13.17	32.55	0	13.17	32.55	24.48
25	.66	33.04	25	.66	33.04	26.52
50	−.93	33.33	50	−.93	33.33	26.82

Station 2503; June 29; latitude 46°13′ N., longitude 49°07′ W.; depth 70 meters; dynamic height 1,937.461 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	14.36	32.64	0	14.36	32.64	24.30
26	1.38	33.04	25	1.60	33.03	26.45
53	−.32	33.21	50	−.25	33.19	26.68

Station 2504; June 29–30; latitude 45°53′ N., longitude 48°28′ W.; depth 97 meters; dynamic height 1,937.455 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	13.41	32.17	0	13.41	32.17	24.14
26	−.03	33.04	25	.15	33.02	26.52
53	−1.16	33.28	50	−1.15	33.25	26.76
79	−.75	33.44	75	−.80	33.41	26.88

TABLE OF OCEANOGRAPHIC DATA—Continued

STATIONS OCCUPIED IN 1937—Continued

Station 2505; June 30; latitude 45°48′ N., longitude 48°16′ W.; depth 116 meters; dynamic height 1,937.455 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	12.77	31.86	0	12.77	31.86	24.03
25	.05	33.05	25	.05	33.05	26.56
51	−1.25	33.33	50	−1.25	33.32	26.82
76	−1.12	33.44	75	−1.15	33.44	26.92
102	−.77	33.60	100	−.80	33.58	27.01

Station 2506; June 30; latitude 45°40′ N., longitude 48°03′ W.; depth 617 meters; dynamic height 1,937.401 meters

Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	12.29	31.59	0	12.29	31.59	23.91
25	.69	33.28	25	.69	33.28	26.70
50	−.41	33.56	50	−.41	33.56	26.95
76	.09	33.87	75	.05	33.85	27.20
100	.78	34.09	100	.78	34.09	27.35
150	1.75	34.36	150	1.75	34.36	27.50
201	2.57	34.59	200	2.55	34.59	27.62
301	3.04	34.70	300	3.05	34.70	27.66
492	3.14	34.76	400	3.10	34.74	27.69
599	3.29	34.84	600	3.30	34.84	27.75

Station 2507; June 30; latitude 45°36′ N.; longitude 47°58′ W.; depth 1,138 meters; dynamic height 1,937.356 meters

Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	13.07	31.88	0	13.07	31.88	23.98
25	5.23	33.68	25	5.23	33.68	26.62
50	2.16	34.10	50	2.16	34.10	27.26
76	2.21	34.37	75	2.20	34.37	27.48
99	2.46	34.48	100	2.45	34.48	27.53
149	2.72	34.62	150	2.75	34.62	27.63
198	2.86	34.68	200	2.90	34.68	27.66
297	3.10	34.77	300	3.10	34.77	27.72
341	3.17	34.80	400	3.20	34.83	27.75
520	3.37	34.86	600	3.35	34.87	27.77
681	3.34	34.87	800	3.35	34.88	27.77
895	3.35	34.89	1,000	3.35	34.90	27.79

Station 2508; June 30; latitude 45°32′ N., longitude 47°52′ W.; depth 1,390 meters; dynamic height 1,937.354 meters

Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	13.39	32.00	0	13.39	32.00	24.01
25	5.97	34.06	25	5.97	34.06	26.84
51	3.35	34.34	50	3.40	34.34	27.34
78	2.98	34.48	75	2.95	34.47	27.49
102	2.95	34.59	100	2.95	34.58	27.57
153	2.77	34.63	150	2.80	34.63	27.62
203	2.89	34.72	200	2.90	34.71	27.69
305	3.17	34.80	300	3.15	34.80	27.73
405	3.45	34.85	400	3.45	34.85	27.74
606	3.46	34.88	600	3.45	34.88	27.76
806	3.34	34.86	800	3.35	34.86	27.76
1,083	3.36	34.90	1,000	3.35	34.89	27.78
1,301	3.30	34.905				

Station 2509; June 30; latitude 45°29′ N., longitude 47°43′ W.; depth 1,673 meters; dynamic height 1,937.387 meters

Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	16.16	33.72	0	16.16	33.72	24.76
25	6.67	34.20	25	6.67	34.20	26.86
51	5.27	34.30	50	5.30	34.30	27.11
79	3.04	34.24	75	3.25	34.24	27.27
101	2.92	34.34	100	2.90	34.33	27.38
152	4.91	34.75	150	4.85	34.73	27.50
203	4.90	34.86	200	4.95	34.86	27.59
304	3.08	34.74	300	3.10	34.74	27.69
393	3.97	34.89	400	3.95	34.89	27.72
589	3.74	34.91	600	3.75	34.91	27.76
785	3.56	34.90	800	3.55	34.90	27.77
980	3.48	34.89	1,000	3.45	34.89	27.77
1,376	3.32	34.91	1,500	3.30	34.90	27.80
1,595	3.30	34.90				

Station 2510; June 30; latitude 45°25′ N., longitude 47°33′ W.; depth 2,294 meters; dynamic height 1,937.417 meters

Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	17.51	34.06	0	17.51	34.06	24.69
25	10.15	34.58	25	10.15	34.58	26.61
50	9.12	34.91	50	9.12	34.91	27.05
78	8.41	34.94	75	8.45	34.94	27.18
101	7.42	34.84	100	7.45	34.84	27.25
151	6.72	34.88	150	6.75	34.88	27.38
202	4.84	34.72	200	4.90	34.72	27.49
303	4.50	34.87	300	4.50	34.87	27.65
405	3.90	34.89	400	3.90	34.89	27.73
605	3.54	34.88	600	3.55	34.88	27.75
806	3.73	34.93	800	3.75	34.93	27.77
1,004	3.49	34.905	1,000	3.50	34.91	27.79
1,502	3.35	34.905	1,500	3.35	34.91	27.80
1,999	3.18	34.915	2,000	3.15	34.92	27.83
2,223	3.11	34.92	(2,500)	3.05	34.92	27.84

Station 2511; June 30; latitude 45°30′ N., longitude 46°39′ W.; depth 2,936 meters; dynamic height 1,937.382 meters

Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	16.88	33.52	0	16.88	33.52	24.42
25	6.88	33.86	25	6.88	33.86	26.55
50	2.68	34.08	50	2.68	34.08	27.19
77	2.52	34.25	75	2.50	34.24	27.34
101	3.32	34.50	100	3.30	34.48	27.46
151	3.50	34.67	150	3.50	34.67	27.60
201	3.59	34.75	200	3.60	34.75	27.65
302	4.02	34.89	300	4.05	34.89	27.71
401	3.58	34.85	400	3.60	34.85	27.73
601	3.85	34.93	600	3.85	34.93	27.76
802	3.67	34.92	800	3.70	34.92	27.78
1,001	3.51	34.91	1,000	3.50	34.91	27.79
1,500	3.30	34.88	1,500	3.30	34.885	27.79
1,998	3.16	34.895	2,000	3.15	34.90	27.81
2,495	2.91	34.92	2,500	2.90	34.92	27.85
2,670	2.81	34.90				
2,892	2.66	34.905				

TABLE OF OCEANOGRAPHIC DATA—Continued

STATIONS OCCUPIED IN 1937—Continued

Station 2512: June 30–July 1; latitude 45°33′ N., longitude 45°56′ W., depth 3,489 meters; dynamic height 1,937.401 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	18.45	33.80	0	18.45	33.80	24.26
25	4.35	33.88	25	4.35	33.88	26.87
51	2.96	34.08	50	2.95	34.07	27.17
78	4.53	34.51	75	4.50	34,48	27.34
101	4.76	34.62	100	4.70	34.62	27.43
152	6.26	34.99	150	6.20	34.99	27.54
203	4.18	34.75	200	4.20	34.75	27.59
304	4.92	34.99	300	4.95	34.99	27.69
406	3.81	34.88	400	3.85	34.88	27.72
607	3.62	34.88	600	3.65	34.88	27.74
806	3.70	34.90	800	3.70	34.90	27.76
1,006	3.39	34.88	1,000	3.40	34.88	27.77
1,505	3.34	34.905	1,500	3.35	34.90	27.79
2,014	3.16	34.905	2,000	3.15	34.91	27.82
2,515	2.90	34.915	2,500	2.90	34.91	27.85
3,012	2.55	24.91	3,000	2.55	34.91	27.88
3,237	2.45	34.895	(3,500)	2.30	34.90	27.89
3,460	2.30	34.905				

Station 2513; July 1; latitude 45°38′ N., longitude 45°08′ W.; depth 4,040 meters; dynamic height 1,937.393 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	19.44	33.80	0	19.44	33.80	24.01
25	6.87	34.00	25	6.87	34.00	26.67
50	3.98	34.28	50	3.98	34.28	27.23
76	4.01	34.40	75	4.00	34.39	27.32
101	4.11	34.54	100	4.10	34.54	27.43
151	4.35	34.69	150	4.35	34.69	27.52
201	4.15	34.76	200	4.15	34.76	27.60
302	4.02	34.88	300	4.05	34.88	27.70
397	3.80	34.87	400	3.80	34.87	27.73
594	3.65	34.89	600	3.65	34.89	27.75
790	3.73	34.92	800	3.70	34.91	27.77
986	3.48	34.88	1,000	3.45	34.89	27.77
1,480	3.30	34.91	1,500	3.30	34.91	27.81
1,976	3.15	34.90	2,000	3.15	34.90	27.81
2,373	3.04	34.88	2,500	2.95	34.89	27.82
2,862	2.73	34.90	3,000	2.65	34.90	27.86
3,353	2.42	34.89	3,500	2.40	34.90	27.88
3,653	2.32	34.90	(4,000)	2.10	34.88	27.88
3,878	2.15	34.88				

Station 2514; July 1; latitude 45°41′ N., longitude 44°24′ W.; depth 4,560 meters; dynamic height 1,937.658 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	21.13	35.12	0	21.13	35.12	24.57
25	16.04	35.39	25	16.04	35.39	26.06
50	13.35	35.28	50	13.35	35.28	26.56
77	12.97	35.30	75	13.00	35.30	26.64
100	12.39	35.23	100	12.39	35.23	26.71
150	12.55	35.49	150	12.55	35.49	26.88
201	11.31	35.38	200	11.35	35.38	27.02
301	6.89	34.76	300	6.95	34.76	27.26
300	6.93	34.76	400	5.95	34.85	27.46
440	5.63	34.86	600	4.10	34.84	27.67
572	4.22	34.84	800	3.85	34.90	27.74
698	3.84	34.87	1,000	3.85	34.92	27.76
1,082	3.86	34.925	1,500	3.40	34.89	27.78
1,487	3.51	34.90	2,000	3.30	34.90	27.80
1,402	3.37	34.885	2,500	3.15	34.91	27.82
1,740	3.33	34.89	(3,000)	2.90	34.91	27.85
2,100	3.27	34.905				
2,476	3.16	34.91				
2,648	3.08	34.92				
2,832	2.98	34.92				

Station 2515; July 1; latitude 46°14′ N., longitude 44°27′ W.; depth 3,475 meters; dynamic height 1,937.318 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	16.80	34.17	0	16.80	34.17	24.94
25	7.80	34.53	25	7.80	34.53	26.95
50	6.51	34.60	50	6.51	34.60	27.19
77	5.89	34.62	75	5.90	34.62	27.29
101	5.26	34.64	100	5.30	34.64	27.37
151	4.60	34.68	150	4.65	34.68	27.48
201	4.12	34.72	200	4.15	34.72	27.57
302	3.44	34.75	300	3.45	34.75	27.66
398	3.12	34.80	400	3.10	34.80	27.74
596	3.06	34.86	600	3.05	34.86	27.79
793	3.18	34.90	800	3.20	34.90	27.81
992	3.18	34.90	1,000	3.20	34.90	27.81
1,489	3.07	34.92	1,500	3.05	34.92	27.84
1,998	2.87	34.915	2,000	2.85	34.92	27.86
2,498	2.63	34.92	2,500	2.65	34.92	27.88
2,994	2.35	34.915	3,000	2.35	34.91	27.89
3,222	2.24	34.91	(3.500)	2.20	34.91	27.91
3,444	2.22	34.91				

Station 2516; July 1; latitude 46°21′ N., longitude 44°24′ W.; depth 1,953 meters; dynamic height 1,937.285 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	13.47	34.24	0	13.47	34.24	25.72
25	6.85	34.36	25	6.85	34.36	26.96
51	5.53	34.48	50	5.55	34.48	27.21
79	5.12	34.73	75	5.20	34.71	27.44
101	4.42	34.77	100	4.45	34.77	27.58
152	4.01	34.82	150	4.05	34.82	27.66
203	3.59	34.83	200	3.60	34.83	27.71
304	3.60	34.88	300	3.60	34.88	27.75
388	3.39	34.88	400	3.35	34.88	27.77
583	3.29	34.89	600	3.30	34.89	27.79
780	3.28	34.90	800	3.25	34.90	27.80
977	3.20	34.89	1,000	3.20	34.89	27.80
1,473	3.14	34.915	1,500	3.15	34.91	27.82
1,650	3.12	34.91				

Station 2517; July 7; latitude 46°58′ N., longitude 44°54′ W.; depth 149 meters; dynamic height 1,937.404 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	16.17	33.90	0	16.17	33.90	24.88
26	5.25	34.22	25	5.50	34.22	27.02
52	3.79	34.30	50	3.80	34.29	27.26
77	3.71	34.38	75	3.70	34.38	27.34
103	3.52	34.38	100	3.55	34.38	27.35
129	3.50	34.46				

Station 2518; July 7; latitude 46°55′ N., longitude 44°30′ W.; depth 168 meters; dynamic height 1,937.413 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	16.14	34.02	0	16.14	34.02	24.98
26	5.07	34.18	25	5.50	34.18	26.98
51	3.95	34.29	50	3.95	34.28	27.24
77	3.65	34.35	75	3.65	34.35	27.33
103	3.61	34.43	100	3.60	34.42	27.39
154	3.66	34.58	150	3.65	34.57	27.50

TABLE OF OCEANOGRAPHIC DATA—Continued

STATIONS OCCUPIED IN 1937—Continued

Station 2519; July 7; latitude 46°54′ N., longitude 44°20′ W.; depth 242 meters; dynamic height 1,937.396 meters

Observed vaues			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	15.65	34.00	0	15.65	34.00	25.07
27	4.70	34.21	25	5.20	34.20	27.04
53	3.67	34.32	50	3.70	34.31	27.29
80	3.65	34.40	75	3.65	34.39	27.35
106	3.54	34.45	100	3.55	34.44	27.41
160	3.26	34.54	150	3.30	34.52	27.50
213	3.28	34.66	200	3.25	34.63	27.59

Station 2520; July 7; latitude 46°53′ N., longitude 44°00′ W.; depth 324 meters; dynamic height 1,937.389 meters

Observed vaues			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	15.06	33.68	0	15.06	33.68	24.96
25	4.46	34.20	25	4.46	34.24	27.15
51	3.69	34.32	50	3.70	34.32	27.30
76	2.97	34.35	75	3.00	34.35	27.39
101	2.51	34.33	100	2.50	34.33	27.41
152	3.11	34.50	150	3.10	34.49	27.49
203	3.31	34.67	200	3.30	34.76	27.69
304	3.83	34.85	300	3.80	34.85	27.71

Station 2521; July 7; latitude 46°51′ N., longitude 43°54′ W.; depth 582 to 576 meters; dynamic height 1,937.370 meters

Observed vaues			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	15.10	33.75	0	15.10	33.75	25.01
25	3.39	34.16	25	3.39	34.16	27.20
50	2.66	34.46	50	2.66	34.46	27.51
79	3.38	34.63	75	3.35	34.62	27.57
101	3.35	34.63	100	3.35	34.63	27.57
151	3.40	34.71	150	3.40	34.71	27.64
202	3.59	34.78	200	3.60	34.77	27.67
303	3.66	34.80	300	3.65	34.80	27.68
370	3.64	34.85	400	3.60	34.86	27.74
588	3.37	34.86	(600)	3.35	34.86	27.76

Station 2522; July 7; latitude 46°48′ N., longitude 43°27′ W.; depth 2,236 meters; dynamic height 1,937.405 meters

Observed vaues			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	17.18	34.28	0	17.18	34.28	24.94
25	8.27	34.80	25	8.27	34.80	27.10
50	7.65	34.85	50	7.65	34.85	27.23
79	7.55	34.95	75	7.55	34.95	27.32
101	6.51	34.85	100	6.55	34.85	27.38
151	5.17	34.83	150	5.20	34.83	27.53
202	4.47	34.82	200	4.50	34.82	27.61
303	3.69	34.80	300	3.70	34.80	27.68
399	3.37	34.82	400	3.35	34.81	27.72
598	3.31	34.80	600	3.30	34.81	27.73
796	3.28	34.84	800	3.30	34.84	27.75
994	3.24	34.84	1,000	3.25	34.84	27.75
1,490	3.22	34.86	1,500	3.20	34.86	27.78
1,935	3.22	34.86	2,000	3.20	34.86	27.78
2,154	3.11	34.86				

Station 2523; July 7; latitude 46°43′ N., longitude 42°41′ W.; depth 3,610 meters; dynamic height 1,937.356 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	17.61	34.15	0	17.61	34.15	24.74
25	7.82	34.31	25	7.82	34.31	26.78
49	5.53	34.52	50	5.50	34.52	27.26
78	4.86	34.64	75	4.90	34.64	27.42
98	4.32	34.64	100	4.25	34.64	27.49
147	3.78	34.74	150	3.80	34.75	27.63
197	4.34	34.88	200	4.35	34.88	27.67
295	4.13	34.90	300	4.15	34.90	27.71
386	*4.27	34.94	400	4.20	34.94	27.74
580	3.59	34.88	600	3.55	34.88	27.75
775	3.46	34.90	800	3.45	34.90	27.78
971	3.44	34.90	1,000	3.45	34.90	27.78
1,464	3.24	34.905	1,500	3.25	34.91	27.81
1,960	3.09	34.92	2,000	3.10	34.92	27.82
2,474	2.76	34.91	2,500	2.75	34.91	27.86
2,970	2.36	34.915	3,000	2.35	34.91	27.89
3,345	2.22	34.89	3,500	2.20	34.89	27.89
3,560	2.19	34.89				

Station 2524; July 7–8; latitude 46°46′ N., longitude 42°04′ W.; depth 4,054 meters; dynamic height 1,937.594 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	19.69	34.46	0	19.69	34.46	24.45
24	15.08	35.50	25	15.00	35.50	26.37
48	13.65	35.46	50	13.50	35.44	26.65
76	12.79	35.33	75	12.80	35.33	26.71
96	13.09	35.60	100	13.05	35.59	26.85
144	11.58	35.40	150	11.40	35.38	27.02
192	10.15	35.24	200	9.95	35.23	27.16
288	6.87	34.88	300	7.05	34.94	27.38
207	9.71	35.22	400	6.30	34.96	27.50
305	7.08	34.945	600	4.40	34.98	27.74
414	6.09	34.96	800	3.95	34.95	27.77
495	5.07	34.98	1,000	3.80	34.93	27.77
1,037	3.75	34.93	1,500	3.40	34.90	27.79
1,284	3.55	34.93	2,000	3.30	34.90	27.80
1,544	3.38	34.90				
1,816	3.31	34.90				
1,941	3.31	34.90				
2,069	3.26	34.905				

Station 2525; July 8; latitude 46°59′ N., longitude 41°33′ W.; depth 4,300 meters; dynamic height 1,937.848 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	20.60	35.77	0	20.60	35.77	25.21
24	17.92	35.84	25	17.85	35.84	25.96
48	15.28	35.82	50	15.15	35.81	26.58
75	14.41	35.70	75	14.41	35.70	26.66
95	14.10	35.70	100	14.05	35.70	26.73
143	13.47	35.70	150	13.40	35.69	26.86
191	12.88	35.64	200	12.80	35.63	26.94
286	12.10	35.58	300	12.05	35.58	27.05
280	12.14	35.60	400	11.35	35.48	27.10
425	11.02	35.44	600	7.45	35.02	27.39
574	7.88	35.04	800	5.20	34.95	27.63
726	5.80	34.96	1,000	4.20	34.92	27.73
1,131	3.90	34.92	1,500	3.60	34.93	27.79
1,566	3.56	34.93	2,000	3.35	34.91	27.80
1,891	3.39	34.905	2,500	3.15	34.91	27.82
2,308	3.27	34.92	3,000	2.85	34.91	27.85
2,740	3.02	34.895	3,500	2.50	34.90	27.87
3,187	2.74	34.92				
3,389	2.58	34.90				
3,598	2.44	34.905				

TABLE OF OCEANOGRAPHIC DATA—Continued

STATIONS OCCUPIED IN 1937—Continued

Station 2526; July 8; latitude 46°50′ N., longitude 40°43′ W.; depth 4,545 meters; dynamic height 1,937.971 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	20.18	35.64	0	20.18	35.64	25.22
23	17.76	35.62	25	17.65	35.62	25.85
46	15.08	35.76	50	14.80	35.75	26.61
75	13.96	35.60	75	13.96	35.60	26.68
92	14.12	35.70	100	14.05	35.70	26.73
138	13.51	35.72	150	13.45	35.73	26.88
183	13.26	35.73	200	13.10	35.72	26.95
275	12.51	35.65	300	12.45	35.65	27.02
290	12.46	35.65	400	12.10	35.60	27.05
438	11.91	35.56	600	9.85	35.25	27.19
587	10.09	35.27	800	6.60	35.02	27.51
739	7.46	35.06	1,000	4.95	34.95	27.66
1,128	4.40	34.945	1,500	3.75	34.93	27.77
1,527	3.71	34.93	2,000	3.40	34.91	27.80
1,969	3.42	34.91				
2,170	3.37	34.92				

Station 2527; July 8–9; latitude 46°33′ N., longitude 40°09′ W.; depth 4,507 meters; dynamic height 1,938.058 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	20.22	35.60	0	20.22	35.60	25.18
24	16.06	35.67	25	16.00	35.67	26.28
48	14.45	35.64	50	14.35	35.64	26.62
76	14.04	35.72	75	14.05	35.72	26.75
95	13.99	35.79	100	13.95	35.79	26.82
143	13.34	35.73	150	13.30	35.73	26.91
190	13.13	35.72	200	13.10	35.71	26.94
285	12.63	35.68	300	12.60	35.68	27.01
348	12.57	35.68	400	12.50	35.67	27.03
530	12.19	35.62	600	11.60	35.51	27.08
717	9.88	35.24	800	8.25	35.10	27.33
909	6.54	34.97	1,000	5.60	34.95	27.58
1,375	3.95	34.925	1,500	3.80	34.92	27.77
1,850	3.56	34.905	2,000	3.45	34.91	27.79
2,097	3.40	34.91	2,500	3.35	34.91	27.80
2,550	3.33	34.915	3,000	3.10	34.90	27.82
3,010	3.09	34.90	3,500	2.80	34.90	27.84
3,484	2.79	34.90	4,000	2.45	34.92	27.89
3,740	2.62	34.91				
3,958	2.49	34.925				

Station 2528; July 9; latitude 47°00′ N., longitude 40°19′ W.; depth 4,554 meters; dynamic height 1,938.006 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	19.67	35.57	0	19.67	35.57	25.30
24	16.64	35.66	25	16.55	35.66	26.15
48	14.42	35.54	50	14.30	35.54	26.56
76	13.99	35.60	75	14.00	35.61	26.68
96	13.83	35.64	100	13.80	35.64	26.74
144	13.36	35.70	150	13.35	35.71	26.89
191	13.52	35.73	200	13.50	35.73	26.87
287	12.53	35.66	300	12.55	35.66	27.01
335	12.52	35.68	400	12.45	35.66	27.03
497	11.95	35.58	600	10.40	35.32	27.15
655	9.43	35.19	800	7.00	35.01	27.45
809	6.91	35.00	1,000	5.30	34.98	27.64
1,209	4.41	34.97	1,500	3.80	34.93	27.77
1,603	3.68	34.92	(2,000)	3.30	34.89	27.79
1,809	3.49	34.90				

Station 2529; July 9; latitude 47°28′ N., longitude 40°22′ W.; depth 4,559 meters; dynamic height 1,937.902 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	19.06	35.57	0	19.06	35.57	25.46
23	19.05	35.56	25	19.00	35.55	25.46
47	14.27	35.53	50	14.15	35.53	26.56
75	13.70	35.58	75	13.70	35.58	26.72
94	13.36	35.59	100	13.35	35.59	26.79
141	13.24	35.69	150	13.10	35.68	26.90
187	12.57	35.61	200	12.55	35.61	26.97
281	12.54	35.66	300	12.50	35.65	27.01
311	12.41	35.64	400	11.85	35.53	27.04
473	10.98	35.40	600	8.40	35.06	27.28
641	7.47	35.00	800	5.30	34.94	27.61
812	5.20	34.94	1,000	4.40	34.93	27.70
1,293	3.82	34.92	1,500	3.70	34.93	37.78
1,825	3.42	34.94	(2,000)	3.30	34.93	27.82

Station 2530; July 10; latitude 47°41′ N., longitude 39°55′ W.; depth 4,570 meters; dynamic height 1,937.654 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	17.31	35.06	0	17.31	35.06	25.50
25	17.09	35.09	25	17.09	35.09	25.58
50	11.25	35.14	50	11.25	35.14	26.86
75	11.07	35.28	75	11.07	35.28	27.00
100	10.69	35.27	100	10.69	35.27	27.06
150	10.12	35.24	150	10.12	35.24	27.14
200	9.56	35.17	200	9.56	35.17	27.18
295	8.17	35.08	300	8.15	35.07	27.33
394	7.11	34.96	400	7.05	34.96	27.40
592	5.02	34.90	600	5.00	34.90	27.62
790	4.28	34.90	800	4.25	34.90	27.70
990	3.94	34.90	1,000	3.90	34.90	27.74
1,482	3.49	34.89	1,500	3.50	34.89	27.77
1,970	3.30	34.895	2,000	3.30	34.90	27.80

Station 2531; July 10; latitude 48°10′ N., longitude 40°07′ W.; depth 4,522 meters; dynamic height 1,937.689 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	18.04	35.06	0	18.04	35.06	25.32
25	17.94	35.08	25	17.94	35.08	25.36
50	11.74	34.88	50	11.74	34.88	26.56
75	9.94	34.82	75	9.94	34.82	26.84
100	10.04	35.04	100	10.04	35.04	26.99
150	9.63	35.09	150	9.63	35.09	27.10
200	8.69	34.98	200	8.69	34.98	27.17
301	8.06	35.01	300	8.10	35.01	27.29
402	6.71	34.91	400	6.75	34.91	27.40
607	4.83	34.90	600	4.90	34.90	27.63
815	4.18	34.90	800	4.20	34.90	27.71
1,025	3.84	34.895	1,000	3.85	34.90	27.74
1,522	3.48	34.86	1,500	3.50	34.86	27.75
2,007	3.31	34.885	2,000	3.30	34.88	27.78

Station 2532; July 10; latitude 48°42′ N., longitude 40°18′ W.; depth 4,451 meters; dynamic height 1,937.844 meters

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
0	18.83	35.57	0	18.83	35.57	25.52
24	17.54	35.56	25	17.50	35.56	25.84
49	13.99	35.44	50	15.95	35.44	26.55
73	13.56	35.43	75	13.55	35.43	26.63
97	13.11	35.38	100	13.15	35.39	26.68
146	13.61	35.66	150	13.60	35.66	26.80
194	12.90	35.60	200	12.85	35.59	26.90
304	*12.02	35.56	300	12.10	35.56	27.02
404	9.69	35.20	400	9.85	35.22	27.17
606	6.10	34.87	600	6.20	34.87	27.45
808	4.49	34.90	800	4.50	34.90	27.67
1,011	3.91	34.895	1,000	3.95	34.90	27.73
1,472	3.54	34.88	1,500	3.55	34.88	27.75
1,904	3.36	34.875	(2,000)	3.35	34.88	27.77

TABLE OF OCEANOGRAPHIC DATA—Continued

STATIONS OCCUPIED IN 1937—Continued

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
Station 2533; July 10; latitude 49°07′ N., longitude 40°26′ W.; depth 4,437 meters; dynamic height 1,937.913 meters						
0	18.15	35.63	0	18.15	35.63	25.74
25	18.13	35.63	25	18.13	35.63	25.74
50	14.47	35.58	50	14.47	35.58	26.55
75	14.41	35.73	75	14.41	35.73	26.68
100	14.28	35.76	100	14.28	35.76	26.73
151	13.75	35.76	150	13.75	35.76	26.84
201	13.40	35.75	200	13.45	35.75	26.90
306	*12.40	35.64	300	12.45	35.65	27.02
408	11.89	35.57	400	11.95	35.57	27.06
612	8.24	35.07	600	8.50	35.09	27.28
816	5.61	34.97	800	5.75	34.97	27.58
1,020	4.62	34.99	1,000	4.70	34.99	27.70
1,530	3.69	34.925	1,500	3.70	34.93	27.78
2,039	3.33	34.91	2,000	3.30	34.91	27.81
Station 2534; July 11; latitude 49°45′ N., longitude 40°35′ W.; depth 4,446 meters; dynamic height 1,937.851 meters						
0	18.96	35.55	0	18.96	35.55	25.47
20	19.13	35.55	25	18.85	35.56	25.50
40	15.36	35.64	50	14.45	35.62	26.59
60	14.06	35.59	75	13.95	35.62	26.69
81	13.95	35.63	100	14.00	35.71	26.75
121	14.07	35.79	150	13.45	35.72	26.88
161	13.23	35.69	200	12.70	35.63	26.96
228	12.45	35.61	300	12.25	35.63	27.04
301	12.27	35.63	400	11.55	35.50	27.08
445	11.03	35.41	600	7.25	34.99	27.39
584	7.57	34.99	800	5.25	34.97	27.65
719	5.79	34.97	1,000	4.45	34.96	27.73
1,079	4.22	34.96	1,500	3.60	34.93	27.79
1,437	3.65	34.935	(2,000)	3.30	34.91	27.81
Station 2535; July 11; latitude 50°23′ N., longitude 40°45′ W.; depth 4,418 meters; dynamic height 1,937.764 meters						
0	17.39	34.55	0	17.39	34.55	25.10
23	18.21	35.36	25	18.20	35.42	25.56
47	16.03	35.66	50	15.75	35.66	26.33
70	14.73	35.65	75	14.60	35.64	26.57
93	14.08	35.56	100	13.95	35.55	26.64
140	13.37	35.51	150	13.25	35.50	26.75
186	12.51	35.42	200	12.45	35.48	26.89
184	13.00	35.59	300	10.35	35.30	27.14
244	11.64	35.44	400	7.95	34.97	27.28
365	8.78	35.06	600	5.85	35.01	27.60
485	6.27	34.86	800	4.65	34.96	27.71
604	5.83	35.02	1,000	3.90	34.92	27.76
935	4.06	34.92	(1,500)	3.50	34.91	27.79
1,286	3.59	34.91	(2,000)	3.30	34.90	27.80

Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
Station 2536: July 11; latitude 51°01′ N., longitude 41°08′ W.; depth 4,278 meters; dynamic height 1,937.628 meters						
0	16.82	34.53	0	16.82	34.53	25.22
21	15.82	35.56	25	15.65	35.55	26.26
42	14.06	35.40	50	13.85	35.38	26.53
63	13.40	35.36	75	13.00	35.33	26.66
85	12.72	35.31	100	12.65	35.36	26.76
127	12.58	35.44	150	12.15	35.43	26.91
169	11.63	35.42	200	11.10	35.32	27.03
183	11.51	35.40	300	6.50	34.75	27.31
242	9.04	35.06	400	5.30	34.70	27.42
358	5.08	34.56	600	4.20	34.89	27.70
471	5.67	34.98	800	3.85	34.90	27.74
581	4.27	34.89	1,000	3.70	34.91	27.77
916	3.76	34.91	(1,500)	3.45	34.92	27.80
1,279	3.50	34.92	(2,000)	3.25	34.91	27.81
Station 2537; July 11–12; latitude 51°37′ N., longitude 41°30′ W.; depth 4,142 meters; dynamic height 1,937.508 meters						
0	13.55	34.48	0	13.55	34.48	25.89
22	12.13	34.60	25	12.05	34.61	26.29
44	9.95	34.88	50	9.80	34.92	26.94
65	9.47	34.96	75	9.25	34.95	27.06
87	8.74	34.94	100	8.05	34.86	27.18
131	6.96	34.71	150	7.80	34.87	27.22
174	8.89	35.16	200	8.10	35.06	27.33
243	6.71	34.88	300	5.45	34.79	27.47
323	5.01	34.78	400	4.55	34.81	27.60
482	4.22	34.86	600	3.95	34.89	27.72
639	3.89	34.90	800	3.80	34.92	27.77
794	3.82	34.92	1,000	3.70	34.91	27.77
1,223	3.50	34.905	1,500	3.40	34.90	27.79
1,673	3.29	34.895	(2,000)	3.25	34.89	27.79
Station 2538; July 12; latitude 52°13′ N., longitude 41°42′ W.; depth 4,273 meters; dynamic height 1,937.400 meters						
0	13.31	34.64	0	13.31	34.64	26.07
25	12.44	34.74	25	12.44	34.74	26.32
50	8.28	34.95	50	8.28	34.95	27.21
76	7.32	34.95	75	7.35	34.95	27.35
101	6.71	34.92	100	6.75	34.92	27.41
151	5.84	34.86	150	5.85	34.86	27.48
202	5.12	34.84	200	5.20	34.84	27.54
310	4.29	34.86	300	4.40	34.86	27.65
413	4.01	34.88	400	4.10	34.88	27.70
619	3.79	34.90	600	3.80	34.90	27.75
826	3.65	34.91	800	3.65	34.91	27.77
1,034	3.48	34.905	1,000	3.50	34.91	27.79
1,549	3.30	34.915	1,500	3.30	34.90	27.80
2,062	3.21	34.89	2,000	3.25	34.89	27.79

TABLE OF OCEANOGRAPHIC DATA—Continued

STATIONS OCCUPIED IN 1937—Continued

Observed values			Scaled values				Observed values			Scaled values			
Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t	Depth, meters	Temperature °C.	Salinity ‰	Depth, meters	Temperature °C.	Salinity ‰	σ_t
Station 2539; July 12; latitude 53°00′ N., longitude 42°21′ W.; depth 3,511 meters; dynamic height 1,937.351 meters							Station 2540; July 12; latitude 54°00′ N., longitude 42°52′ W.; depth 3,544 meters; dynamic height 1,937.390 meters						
0	12.13	34.85	0	12.13	34.85	26.46	0	10.21	34.79	0	10.21	34.79	26.77
25	8.15	34.88	25	8.15	34.88	27.17	23	9.88	34.78	25	9.70	34.78	26.85
51	6.61	34.86	50	6.65	34.86	27.38	45	6.56	34.90	50	6.30	34.89	27.44
76	5.92	34.86	75	5.95	34.86	27.47	68	5.85	34.85	75	5.70	34.85	27.49
101	5.43	34.83	100	5.45	34.83	27.50	90	5.46	34.85	100	5.40	34.85	27.53
152	4.94	34.82	150	4.95	34.82	27.56	135	5.27	34.86	150	5.20	34.86	27.56
203	4.59	34.83	200	4.60	34.83	27.60	180	5.15	34.845	200	5.15	34.85	27.56
307	4.07	34.85	300	4.10	34.85	27.68	262	5.07	34.88	300	5.00	34.86	27.59
410	3.90	34.88	400	3.90	34.88	27.72	352	4.72	34.84	400	4.50	34.84	27.62
616	3.73	34.91	600	3.75	34.91	27.76	535	4.08	34.87	600	4.00	34.89	27.72
823	3.59	34.91	800	3.60	34.91	27.78	725	3.83	34.915	800	3.75	34.91	27.76
1,030	3.42	34.90	1,000	3.45	34.90	27.78	920	3.62	34.89	1,000	3.55	34.89	27.76
1,541	3.28	34.89	1,500	3.30	34.89	27.79	1,411	3.31	34.91	1,500	3.30	34.91	27.81
2,049	3.19	34.89	2,000	3.20	34.89	27.80	1,923	3.25	34.90	2,000	3.25	34.90	27.80

Contribution No. 191

SHOAL-WATER DEPOSITS OF THE BERMUDA BANKS

BY

JEAN P. TODD

Reprinted from Sedimentary Petrology for April, 1939

JOURNAL OF SEDIMENTARY PETROLOGY, VOL. 9, NO. 1, PP. 8–13, FIG. 1, TABLES 1–2,
APRIL, 1939

SHOAL-WATER DEPOSITS OF THE BERMUDA BANKS*

JEAN P. TODD
Harvard University

ABSTRACT

Mechanical analyses of pure calcareous sediment from the Bermuda Banks show a correlation between mechanical composition and topographic location. Beach sands are well sorted and uniform, lagoon sediment is fine and slightly less well sorted, and the sands of the exposed boundary reef are coarse. The size frequency distributions are similar to those to be expected in inorganic sediment produced by the sea in like environments.

INTRODUCTION

The present study of recent calcareous bottom deposits off the Bermuda Islands was undertaken with a two-fold purpose: (1) to determine any correlation existing between mechanical composition and topographic location, and (2) to add to the few existing analyses of pure calcareous sediment to determine whether such material is similar in mechanical composition to inorganic sediments of like environment. The samples were collected in 1934 by Mr. H. C. Stetson with these two purposes in mind and were later placed at the disposal of the writer for analysis. Invaluable aid was given by Mr. Stetson throughout the laboratory work and during the preparation of the manuscript.

The isolation of the Bermuda Islands from any land mass precludes the addition of any appreciable amount of inorganic detritus to the sediment (Sayles, 1931). The Islands themselves as well as the surrounding reefs are completely calcareous. The area is well chosen for a study of present sedimentation for all material is produced, transported, and deposited in this one place under observable conditions. The "controls" are, therefore, all known and no factors are left to be explained as characteristics resulting from past and only partially known environments. The present areas of sedimentation of the Bermuda Banks (Fig. 1) lend themselves to classification in five topographic divisions, (1) the beaches, (2) the inner, more or less enclosed lagoons, (3) the outer lagoon, (i.e. the area of shoals and flats within the boundary reef), (4) the boundary reef, and (5) the area outside the reef and within the 100 meter line.

PREVIOUS WORK

Previous work on the recent sediments of the Bermudas is limited to that of Bigelow (1905). He, however, approached the study almost wholly from the viewpoint of the organic derivation of the sediment. He used topographic divisions similar to those above, and though without mechanical analyses, made valuable observations upon grain size and its relation to topography as well as to its source.

Three other studies of mechanical analyses of calcareous sediments have come to the attention of the author. Bramlette (1926) studied thirty samples from Pago Pago Harbor, Samoa. The deposits of the reef flats and slopes are very poorly sorted, with a wide range in sizes, but with only a negligible quantity of material below very fine sand size. The silts of the deeper quiet waters of the inner harbor and the fine sands at the mouth of the harbor are much better sorted than the reef deposits. These conclusions are not all in accord with those of the present investigation. The two areas are however not completely comparable, one being localized in a single harbor and receiving appreciable amounts of inorganic detritus, the other covering a much greater range of environments and containing only calcareous material. There is a similarity between the two

---

* Contribution 191 of the Woods Hole Oceanographic Institution.

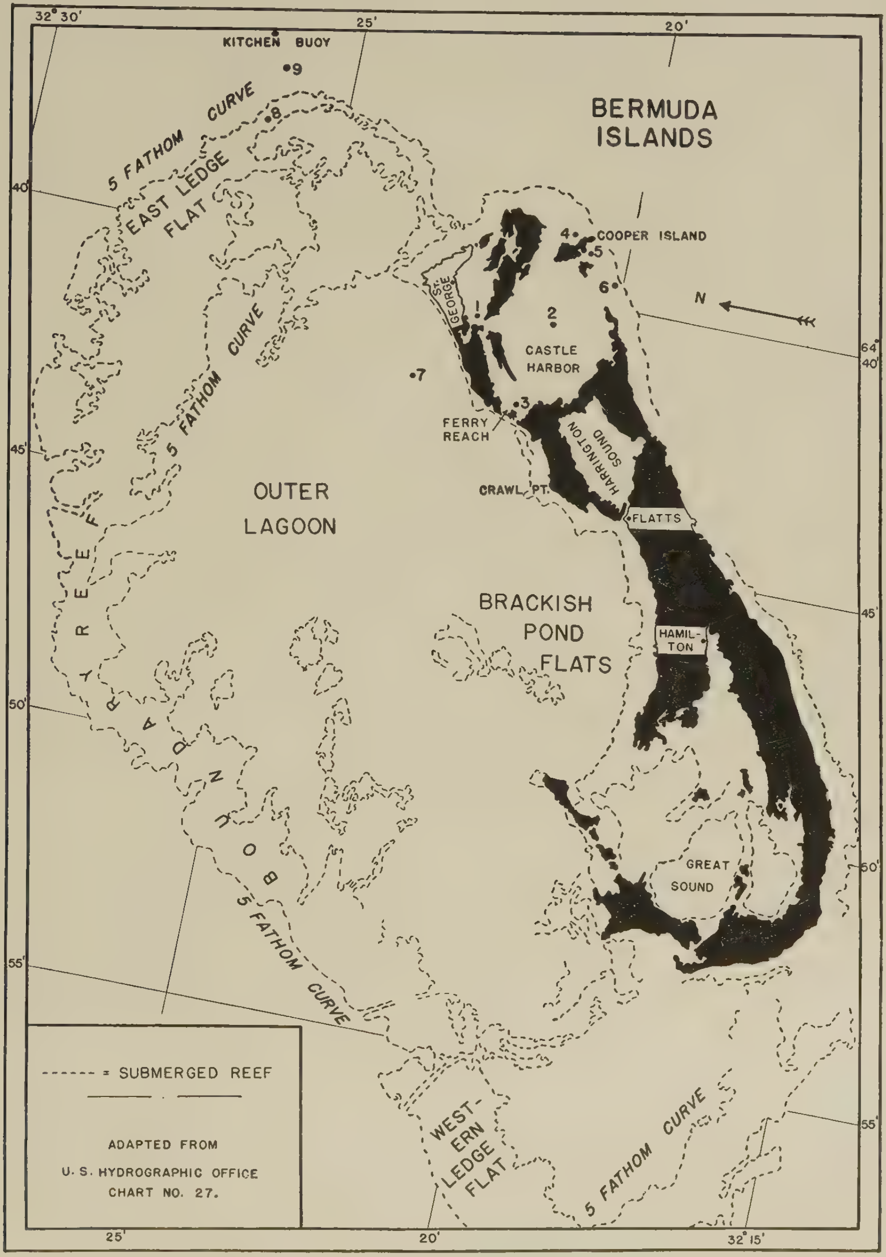

32° 30'
25'
20'
KITCHEN BUOY
•9
BERMUDA ISLANDS
5 FATHOM CURVE
8
EAST LEDGE FLAT
40'
4•
COOPER ISLAND
5
6
N
ST. GEORGE
1
2
CASTLE HARBOR
64° 40'
•7
5 FATHOM CURVE
3
FERRY REACH
HARRINGTON SOUND
45'
OUTER LAGOON
CRAWL PT.
FLATTS
BRACKISH POND FLATS
45'
HAMIL-TON
REEF
50'
YARD
NOB
5 FATHOM CURVE
GREAT SOUND
50'
55'
------ = SUBMERGED REEF
ADAPTED FROM U. S. HYDROGRAPHIC OFFICE CHART NO. 27.
WESTERN LEDGE FLAT
5 FATHOM CURVE
55'
25'
20'
32° 15'

Fig. 1.—Map of Bermuda Islands.

studies however, in the relative coarseness of the sediment on the reef. Bramlette's observation "that a considerable proportion of the material is not comminuted, but remains the size of the original contributing element, and such material when not sufficiently reworked, shows sizes depending to this extent on the contributing materials at the particular place," seems an important concept in the study of detritus of organic origin. It may possibly be used to explain the erratic nature of the statistical constants of one or two of the Bermuda analyses.

Vaughan (1918) analyzed twenty-five samples from Murray Island, Australia; Florida; and the Bahamas. The beaches of Murray Island and Florida contain coarser material than the Bermuda beaches. In comparison with the lagoon sediments of Bermuda the lagoon sands of Australia are coarse, the Florida lagoon deposits similar and the Bahaman bight sediments fine. In all the samples except those of the land-locked areas of the Bahamas, such as South Bight, the clay-silt fractions form a very small per cent. Their absence is ascribed to the winnowing action of currents. A similar lack of fine material, probably resultant from the same cause, is noted in two of the topographic divisions of the Bermuda Banks (Table 2).

Thorp (1936) also finds that in pure calcareous sediments of the Pearl and Hermes Reef the coarsest material lies on or near the reef proper. Five samples are actually gravels (over 50% coarser than 2 mm.). There is a gradual decrease in the size of the material toward the center of the lagoon, but even here, the clay-silt fraction totals less than 18%. The deficiency of fine particles is explained by their easy removal into the deeper waters outside the reef because of the prevailing set of the currents. This study most closely parallels the present one in type of area and results.

MECHANICAL ANALYSES

The laboratory procedure for the analysis of samples containing only material of sand grades and coarser consisted of the removal of salts through repeated washings, sieving for fifteen minutes in a nest of Tyler Standard Screens and the weighing of the separated fractions. Samples containing material in the clay-silt sizes were wet-sieved through the 200-mesh screen. The coarse separate was treated as above. The fine material was freed of salt by a vacuum pump and a series of Pasteur filters and then analyzed according to the pipette method of Krumbein (1932, 1935). Data thus obtained were plotted as cumulative curves, and the median, and Trask's (1932) coefficients of sorting and skewness were determined. These are recorded in Table 1.

From this table it is observed that the beach samples are the most uniform group, with an average median of 0.283 mm., a *So* of 1.28 and a *Sk* of 1.03. The medians are the smallest found in any of the five topographic divisions. All of the beach samples, however, come from one locality, Cooper Island. It is probable that the key to the fineness here has been found by Bigelow (1905, p. 567). He notes that most of the Bermuda beaches are swept clean of calcareous silt, but that some, among them those of Cooper's Island, consist of typical shell sand plus large proportions of calcareous material derived from the destruction of neighboring cliffs. The ledges and cliffs of the Bermuda Islands are all formed of eolianite, a lithified dune sand. The assumption that the mechanical composition of the eolianite is similar to that of the dune sands now forming, seems fair. The very close agreement of the statistical constants of the modern dune sand and beach deposits (Table 1) certainly suggests that the source of the beach material is at least in part the eolianite. Hence the beaches of Cooper Island may show fine medians because of their derivation to a large extent from a wind worked sand, and other Bermuda beaches composed of shell sands in the first cycle of sedimentation, may be coarser. They might then agree with

TABLE 1.—*Statistical Constants*

	No.	Station Location	Depth in Ft.	Q_1 mm.	M mm.	Q_3 mm.	*So*	*Sk*	Log *Sk*
Beach		High tide, Cooper's I. Bar N. End		.38	.28	.22	1.33	1.08	.03
		High tide, Cooper's I. Bar S. End		.29	.24	.21	1.19	1.08	.03
		Low tide, Long Bay Beach, Cooper's I. N. End		.66	.47	.32	1.44	.94	−.03
		Low tide, Long Bay Beach, Cooper's I. S. End		.37	.27	.21	1.33	1.07	.03
		Off-shore, Long Bay Beach, Cooper's I.	2–3	.26	.21	.17	1.25	1.03	.01
		Dunes, Long Bay Beach, Cooper's I. Bar		.28	.25	.21	1.16	.97	−.02
Inner Lagoons	4	Cooper's I. off-shore	6	.24	.21	.19	1.24	1.04	.02
	2	Castle Harbor	30	2.25	1.30	.67	1.84	.89	−.05
		Harrington Sound	48	.92	.25	.04	1.56	.58	−.24
	3	Ferry Reach	20	.92	.56	.21	2.09	.62	−.21
	1	St. George's Harbor	42	.02	.014	.011	1.35	.98	−.01
Outer Lagoon		Crawl Point	24	.76	.56	.42	1.35	1.01	.00
		Brackish Pond Flats	6	.91	.65	.47	1.39	1.01	.00
		Outside Brackish Pond Flats	42	1.25	.61	.08	1.25	.27	−.57
		Outside Murray Anchorage	48	1.10	.70	.38	1.70	.85	−.07
	7	Murray Anchorage	49	.63	.20	.03	4.51	.49	−.31
		Outside Flatts Harbor	28	.84	.55	.26	1.82	.71	−.15
Boundary Reef	5	Inside Reef, Cooper's I.	30	.40	.31	.28	1.19	1.13	.05
	8	East Ledge Flat	24	1.05	.72	.50	1.45	1.02	.01
	9	Kitchen Buoy Reef	60	1.05	.77	.57	1.36	1.01	.00
Outside Reef	6	Outside Reef, Cooper's I.	69	1.00	.70	.58	1.32	1.18	.07
		Kitchen Buoy	54	.20	.14	.11	1.35	1.12	.05

Vaughan's analyses, in which the beach sands were the coarsest of those of any of his environments.

It may be noted in passing that the samples taken at low tide are more poorly sorted and with coarser medians than those taken at high tide. This accords with the findings of Schalk (1938) for the beaches of Cape Cod, but is the reverse of that of Bramlette (1926) for the Aua Reef sands of Samoa.

The first analysis (No. 4) of the inner lagoon group, quite characteristically belongs with the beach sands. This is explained by its position immediately off-shore in only six feet of water. All other inner lagoon samples have a negative log. *Sk*, denoting a frequency curve which tails off farther in the direction of the fine sizes. Though quantitative data are lacking, undoubtedly a very important factor in the reduction of detritus to fine sizes is the passage of bottom sediment through the alimentary tracts of benthonic organisms, especially holothurians. The lagoons are the chosen habitat of such animals.

Castle Harbor sediment is coarser than the other inner lagoon samples. Its median shows it, in fact, to be a fine gravel. Although Castle Harbor is an enclosed lagoon it maintains free communication on all sides with the ocean. Protection from storm waves is thus provided without destroying circulation, and it is therefore a very favorable location for the growth of marine organisms. An abundance of empty shells and organic fragments, which are but little water-worn, give evidence of recent and rapid

TABLE 2.—*Size Fractions*

	No.	Station Location	Gravel 30–1 mm.	Sand 1–.05 mm.	Silt .05–.005 mm.	Clay .005–.001 mm.	Colloid .001–0 mm.
Beach		High tide, Cooper's I. Bar N. End	0	100	0	0	0
		High tide, Cooper's I. Bar S. End	0	100	0	0	0
		Low tide, Long Bay Beach, Cooper's I. N. End	8	92	0	0	0
		Low tide, Long Bay Beach, Cooper's I. S. End	0	100	0	0	0
		Off-shore, Long Bay Beach, Cooper's I.	0	100	0	0	0
		Dunes, Long Bay Beach, Cooper's I. Bar	0	100	0	0	0
Inner Lagoons	4	Cooper's I. off-shore	0	100	0	0	0
	2	Castle Harbor	60	32	4	3	1
		Harrington Sound	22	48	22	6	2
	3	Ferry Reach	21	68	6	3	2
	1	St. George's Harbor	0	0	95	3	2
Outer Lagoon		Crawl Point	15	85	0	0	0
		Brackish Pond Flats	20	80	0	0	0
		Outside Brackish Pond Flats	33	45	13	6	3
		Outside Murray Anchorage	30	68	0.5	0.5	1
	7	Murray Anchorage	10	61	28	0.5	0.5
		Outside Flatts Harbor	12	81	2.5	2	2.5
Boundary Reef	5	Inside Reef, Cooper's I.	0	100	0	0	0
	8	East Ledge Flat	28	72	0	0	0
	9	Kitchen Buoy Reef	28	72	0	0	0
Outside Reef	6	Outside Reef, Cooper's I.	25	75	0	0	0
		Kitchen Buoy	2.5	83.5	8	6	0

accumulation. The somewhat poorer sorting also supports the absence of extensive reworking and attrition. Thus the effect of the original size of the contributing element may be a factor here in explaining the coarseness of the sediment. A second factor is the removal, by tides and currents, of whatever fine material may be formed; for Castle Harbor is too exposed and too large to permit the existence of the quiet water necessary for the settling out of particles of clay and silt sizes. These fine sizes can find ultimate lodging only when carried into more nearly land-locked basins such as St. Georges Harbor. The sediment there is, in fact, fine and extremely well sorted, supporting the idea of longer transport and selective deposition. That the fineness of the material is to be explained by the influx of much material of subaerial erosion (Bigelow, 1905, pp. 268–269) seems improbable because of the lack of surface drainage throughout the Bermudas and because of a lack of vigorous wave action in a lagoon of such limited dimensions as St. Georges Harbor.

The samples of the outer lagoon, with the exception of that of Murray Anchorage, are coarser than those of either of the preceding environments. The deviation of this one sample is reflected in sorting and skewness as well as in the median, and is not readily explained. It may be due merely to chance sampling. The other samples show a high degree of uniformity in both size and sorting. The average median is 0.61 mm. *So*, 1.503, and *Sk*, 0.849. There are positive and negative values for log. skewness, but the negative ones are much greater.

The boundary reef contains the coarsest sediment of any of the environments, with the exception of the Castle Harbor gravel which has been explained above. Though the medians are not much larger than those of the outer lagoon samples, a difference exists between the sediments of the two areas. Table 2 incates that clay and silt sizes are entirely absent on the reef. This is due to its exposed position. The fineness of sample No. 5 may again be due to chance sampling in the lee of a ledge or some other protected spot.

The two samples taken beyond the reef diverge noticeably in their coefficients. One resembles the sediment of the reef itself, the other is inexplicably fine.

From the data it is clear that in general a correlation does exist between mechanical composition and topographic location. The lagoons are areas for the accumulation of fine sediment. The reef sediment is coarse both because it is the source of supply and because it is subjected to the most severe wave and current action of any of the environments. The beaches, as is customary, are the seat of excellent sorting and uniformity. There are of course exceptions to these generalizations, such as occur in any suite of samples, and conclusions must be drawn only from general trends.

The medians of the entire group of samples range from 0.77 mm. to 0.14 mm., with the exception of the Castle Harbor gravel and the St. Georges Harbor silt. Thus the samples are all medium or fine sand. The sorting is good everywhere except at Murray Anchorage, some samples being even extremely well sorted. The range 1.19 to 2.09 falls wholly below Trask's upper limit of 2.5 for good sorting. Good sorting is an indication of the activity and uniform competency of the present agents of erosion, transportation and deposition, and of the adjustment of a sediment to its present environment. Approximately one-half of the samples show a −log. *Sk* and one-half a +log. *Sk*. This agrees with Trask's analysis of samples from all over the world in which skewness tended to be symmetrical about unity.

It may therefore by concluded that calcareous materials obey the same laws as inorganic materials, and result in sediments of similar mechanical composition; and that the sea will produce, under given conditions, sediments of like nature regardless of differences in source and type of supply.

REFERENCES

BIGELOW, H. B., *1905*, The shoal-water deposits of the Bermuda Banks: *Proc. Am. Acad. Arts and Sciences*, 40, 559–591.

BRAMLETTE, M. W., *1926*, Some marine bottom samples from Pago Pago Harbor, Samoa. Carnegie Inst. Wash., Pub. 344, 12–23.

KRUMBEIN, W. C., *1932*, Mechanical analyses of fine-grained sediments: *Jour. Sed. Pet.*, 2, 140–149.

———, *1935*, A time chart for mechanical analyses by the pipette method: *Jour. Sed. Pet.*, 5, 93–95.

SAYLES, R. W., *1931*, Bermuda during the ice age: *Proc. Am. Acad. Arts and Sciences*, 66, 440–444.

SCHALK, MARSHALL, *1938*, A textual study of the outer beach of Cape Cod, Massachusetts: *Jour. Sed. Pet.*, 8, No. 2, 41–54.

THORP, E. M., *1936*, The sediments of the Pearl and Hermes Reef: *Jour. Sed. Pet.*, 6, 109–118.

TRASK, P. D., *1932*, The Origin and Environment of Source Sediments of Petroleum, pp. 70–76, Gulf Publishing Co., Houston, Texas.

VAUGHAN, T. W., *1918*, Some shoal-water bottom samples from Murray Island, Australia, and comparison of them with samples from Florida and the Bahamas: Carnegie Inst. Wash., Pub. No. 213, 243–288.

Contribution No. 192

Sonderdruck aus „Gerlands Beiträge zur Geophysik“, Bd. 54, Heft 4, 1939
Akademische Verlagsgesellschaft m. b. H. in Leipzig

Die Verwendung der Verteilung von Sauerstoff auf die physische Ozeanographie des Karibischen Meeresgebietes¹).

Von
H. R. Seiwell, Sc. D. (M. I. T.)

(Mit 3 Figuren.)

Beitrag Nr. 192 Woods Hole Oceanographic Institution.

Das Karibische Meeresgebiet (ungefähr zwischen den Breitegraden 10°—20° N und den Längengraden 61°—87° W gelegen) ist in zwei natürliche und bathymetrische Unterabteilungen geteilt (Fig. 1), getrennt durch einen Kamm (oft weniger als 1000 m tief), der sich von Honduras nach Haiti über Jamaica erstreckt; das östliche Becken hat man das Karibische Becken (Caribbean basin) und das westliche das Cayman-Becken (Cayman basin) genannt. Die Verbindung zwischen dem Karibischen Becken und dem angrenzenden Atlantischen Ozean wird durch Straßen zwischen den Kleinen Antillen (im allgemeinen nicht tiefer als 1000 m), durch die Mona-Passage (weniger als 1000 m tief) und durch die Anegada-Passage aufrecht (1500—2000 m tief) gebildet. Das Cayman-Becken und das Karibische Becken sind bei dem obengenannten Kamm durch zwei Kanäle von einer 2000 m nicht überschreitenden Tiefe verbunden, und das erstere hat eine Verbindung mit dem offenen Atlantischen Ozean durch die Windward-Passage, dessen größte Tiefe etwas über 3000 m zu sein scheint. Das Wasser des Karibischen Meeresgebietes fließt in den östlichen Teil des Mexikanischen Golfes durch den Yukatankanal (größte Tiefe nur wenig über 2000 m) und wird dann durch eine Schwelle, die weniger als 1000 m tief sich quer über die Floridastraße erstreckt, von den tieferen Teilen des offenen Atlantischen Ozeans getrennt. Da große Areale des Karibischen Beckens tiefer als 4000 m sind und Tiefen von mehr als 6000 m im Cayman-

---

[1] Application of the distribution of oxygen to the physical oceanography of the Caribbean Sea region. H. R. Seiwell: Papers in Physical Oceanography and Meteorology. Vol. VI, No. 1, 60 pp. Sept. 1938.

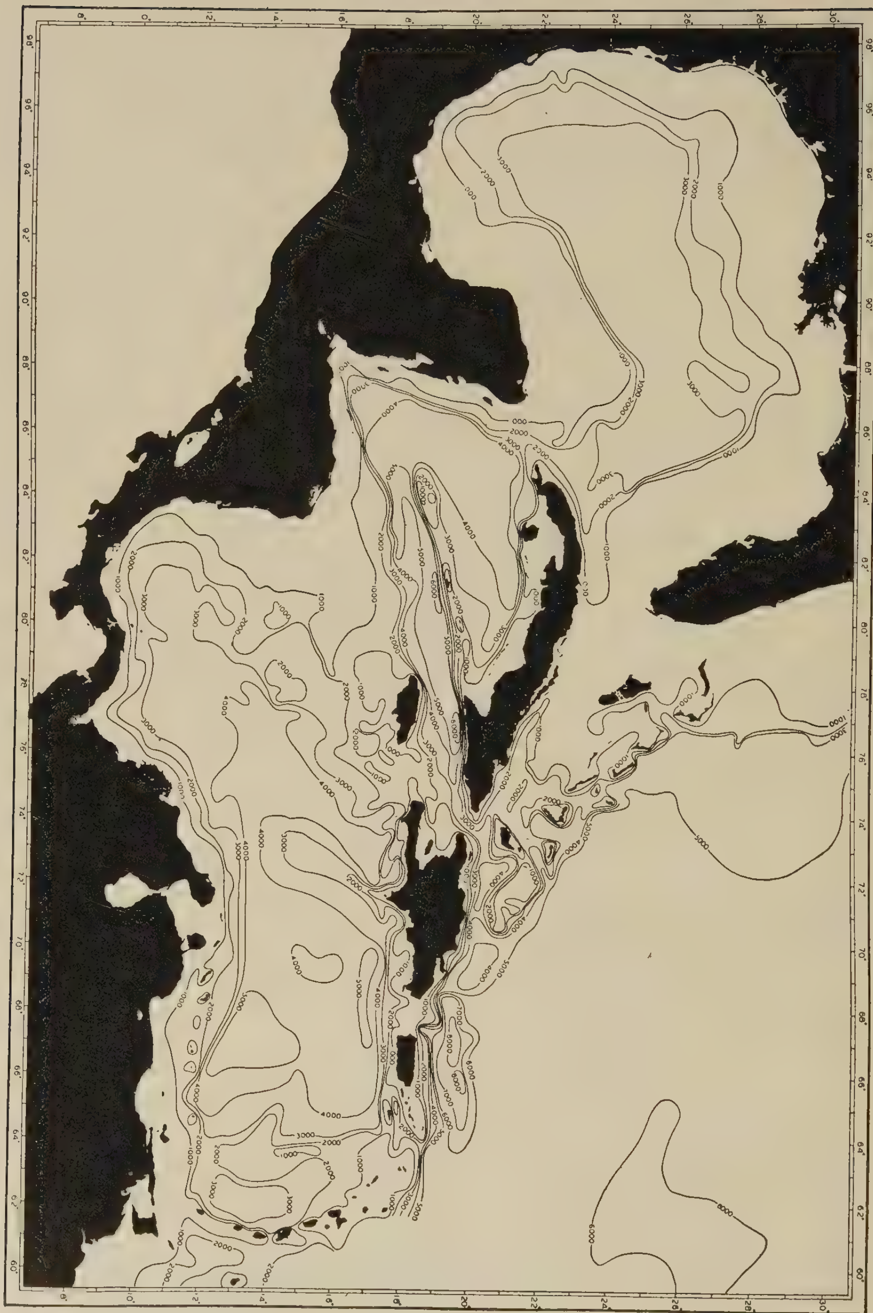


Fig. 1. Übersichtskarte der Tiefenverhältnisse des Karibischen Meeresgebietes.

Becken vorkommen, hat ein großer Teil beider Becken keine direkte Verbindung mit dem angrenzenden Atlantischen Ozean.

Der Sauerstoffgehalt in dem Karibischen Meeresgebiet (4.0 bis 5.0 ccm/liter) wird im wesentlichen in der oberen Schicht bis zu einer Tiefe von 100 m von der biologischen Aktivität kontrolliert, unter welcher Tiefe er zu Minimumwerten sinkt (2.8 zu 3.2 ccm/liter), in der Nähe von 600 m; im Cayman-Becken waren die Minimumwerte 0.1 bis 0.2 ccm/liter höher als im Karibischen. In noch tieferem Wasser (unter dem Minimum) nahm der Gehalt an Sauerstoff in beiden Becken zu, zuerst schnell bis zu Tiefen von 1500—2000 m, und dann langsamer bis zum Boden. Das Cayman-Becken (das an O_2 reichere der zwei Becken) enthielt durchschnittlich 0.5 ccm mehr pro liter in 1500 m Tiefe und 0.71 ccm mehr pro liter als das Karibische zwischen 2000 und 4500 m (Fig. 2). Das Wasser beider Becken enthielt bezeichnender-

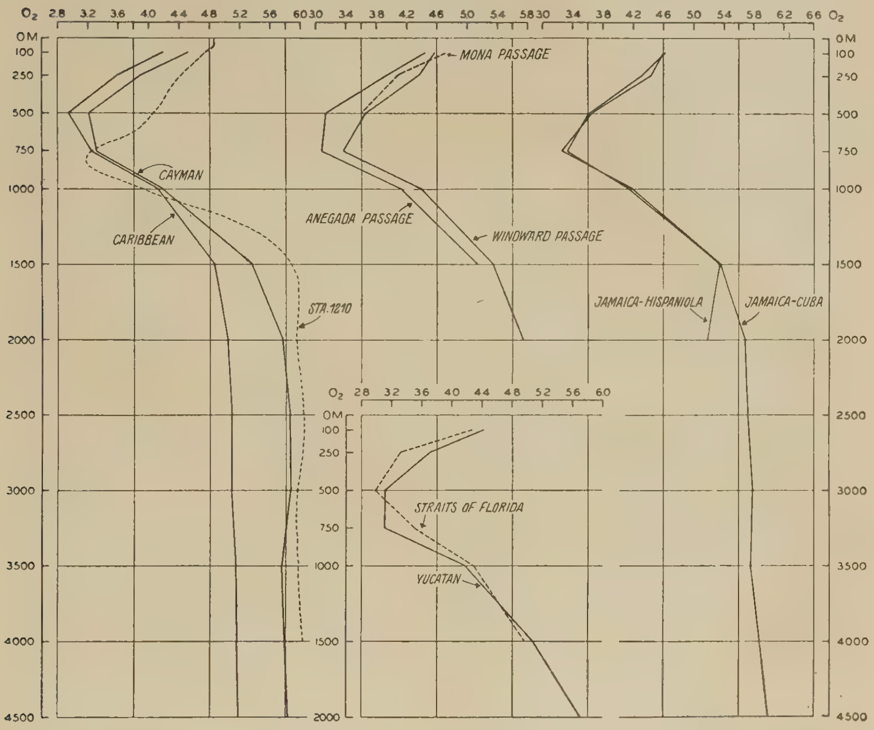


Fig. 2. Mittlere Vertikalverteilung des Sauerstoffgehalts im Karibischen Meeresgebiet.

weise weniger Sauerstoff in Tiefen unter 1000 m als das umgebende Atlantische Wasser in entsprechenden Tiefen; in 1500 m Tiefe enthielt das Cayman-Becken durchschnittlich ungefähr 0.5 ccm weniger pro liter, das Karibische ungefähr 0.9 ccm weniger pro liter. Diese Verhältnisse deuten darauf hin, daß das Wasser keiner der beiden Becken stagnierte.

Die Verbindung von Sauerstoff und Salzgehaltwerten zu Sauerstoff-Salzgehaltsbeziehungen waren nützlich, um gewisse hauptsächliche Wasserbewegungen (zwischen Tiefen von 200—1000—1200 m) im untersuchten Karibischen Meeresgebiet aufzuspüren. Daher erlaubten die Sauerstoff-Salzgehaltsbeziehungen des angrenzenden Atlantischen Wassers, das, wenn es in das Karibische Gebiet einfließt, bestimmte regionale Merkmale aufweist, die Feststellung einer fundamentalen charakteristischen Verteilung innerhalb des Karibischen Gebietes, dessen kleinere Umgestaltungen für die Zirkulation bezeichnend sind. Im Karibischen Becken offenbaren die Sauerstoff-Salzgehaltsbeziehungen basiert auf drei transversale Profile, beinahe gleichartige Variationen an entsprechenden Breitengraden; bedeutsame Veränderungen in der Richtung der hauptsächlichen Wasserströmungen in den oberen Schichten entstehen im besonderen durch kleine Verminderungen des Sauerstoffgehaltes in der Tiefe der Minimumkonzentration an Sauerstoff, und durch Steigerungen des Salzgehaltes in der Tiefe der Minimumkonzentration des Salzgehaltes. Der augenscheinlich weit verbreitete Einfluß von subantarktischem Wasser im Karibischen Meeresgebiet scheint durch das mittlere Salzgehaltsminimum bestimmt zu sein; ein Vergleich der Sauerstoff-Salzgehaltsbeziehungen im Karibischen Meeresgebiet mit jenen, die das angrenzende Atlantische Wasser charakterisieren, deuten darauf hin, daß im erstgenannten die Wassermassen, die aus dem Atlantischen Ozean von Norden und Nordosten zugeführt werden, im wesentlichen in mittleren Tiefen durch Wassermassen, die aus dem Atlantischen Ozean aus Osten und Südosten einströmen, ersetzt werden.

Im Cayman-Becken weisen die Sauerstoff-Salzgehaltsbeziehungen darauf hin, daß der größere Sauerstoffgehalt der oberen Schichten auf die reichere Zufuhr Atlantischen Wassers zurückzuführen war, da dieses nach Durchfluß durch die Windward-Passage hauptsächlich nach rechts abbiegt, um sich dann mit dem Karibischen Hauptstrom zu mischen. Noch westlicher konnte man die Wassermassen des Karibischen Hauptstromes, nachdem sie sich von der Nachbarschaft der

Windward-Passage entfernt hatten, durch ihre Sauerstoff-Salzgehaltsbeziehungen durch den Yucatan-Kanal in den östlichen Teil des Mexikanischen Golfes (wo sie einen großen Wirbel im Sinne des Uhrzeigers zu bilden scheinen) verfolgen, von wo sie sich endlich durch die Floridastraßen bewegen, um als Golfstrom in nördlicher Richtung abzufließen.

Wegen der weiten Verbreitung und der nahen vertikalen Verwandtschaft zwischen den hauptsächlichen Salzgehalt- und Sauerstoffminimumkonzentrationen sind beide Eigenschaften zu einer Untersuchung des vertikalen Austauschkoeffizienten (vertical eddy diffusion coefficient) in den mittleren Tiefen des Karibischen Beckens verwendet worden. Die Berechnung basiert auf der Veränderung von Sauerstoff und Salzgehalt im östlichen Teile dieses Beckens und gab einen Wert von $A = 2.81$ C.G.S.-Einheiten für den senkrechten Turbulenzkoeffizienten und eine mittlere horizontale Geschwindigkeit des Wassers in mittleren Tiefen von $\mu = 2.0 \text{ cms} \cdot \text{sec}^{-1}$. Der auf diese Weise erhaltene Wert des Verhältnisses A/μ wurde durch eine zweite Methode bestätigt und scheint für die betreffenden Tiefen annähernd korrekt zu sein; die berechneten Veränderungen im Salzgehalt und in der Temperatur, als Ergebnis eines senkrechten Turbulenzkoeffizienten von 2.8 C.G.S.-Einheiten, zeigen auch gute Übereinstimmung mit den beobachteten Veränderungen. Die Wirkung einer lateralen Turbulenz scheint in den mittleren Tiefen dieses Gebietes sehr klein zu sein; eine Anwendung der lateralen Ausbreitungsgleichung zeigte (in dem vorliegenden Fall), daß laterale Turbulenzkoeffizienten von 10^5 C.G.S.-Einheiten wirklich vorhanden sein können, aber nur 4% der beobachteten Veränderung (oder eine nicht meßbare Größe) in der Temperatur und im Salzgehalt hervorrufen.

Die Minimumkonzentration an Sauerstoff (Fig. 3) war am kleinsten in den Gebieten, die von den Sunden am weitesten entfernt waren (die Abnahme ist darauf zurückzuführen, daß der Sauerstoffverbrauch größer war als die Zufuhr durch turbulente Mischung), und war im allgemeinen höher im Cayman-Becken als im Karibischen Meer. Um die Abhängigkeit der Minimumkonzentration an Sauerstoff von der Zirkulation zu schätzen, wurde ein Vergleich zwischen ihrer waagerechten Variation und den Abweichungen von der durchschnittlichen Salzgehaltsanomalie vorgenommen. Es ergab sich ein Korrelationskoeffizient von 0.387 für das Karibische Becken und ein Koeffizient von 0.323 für das Cayman-Becken. Diese Resultate führen zur Folgerung, daß der tatsächliche Wert der Minimumkonzentration an Sauerstoff mehr von der biologischen Aktivität als von der Zirkulation abhängig war. Eine statistische Behandlung der Häufigkeitsverteilung der Dichte, an der die Minimumkonzentration an Sauerstoff (in beiden Becken) beobachtet wurde, deutet darauf hin, daß die beobachtete Variation der Dichte ein Ergebnis davon ist, daß man die Proben aufs Geratewohl genommen hatte. Der Scheitelwert der Dichtevariation,

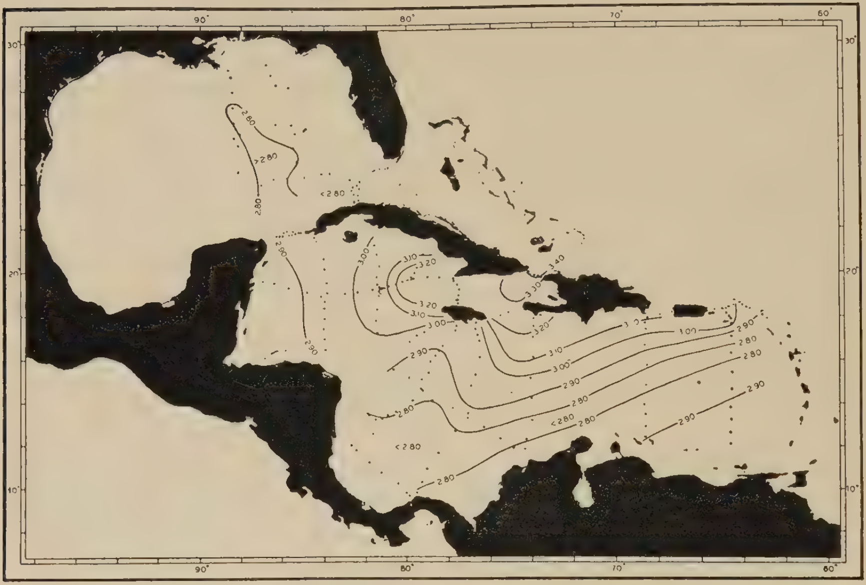


Fig. 3. Verteilung der Minimumkonzentration an Sauerstoff im Karibischen Meeresgebiet.

an der die Minimumkonzentration an Sauerstoff im Karibischen Meeresgebiet vorkam, wurde berechnet zu: $\sigma_t = 27 \cdot 171 \pm 0.007$; dies zeigt gute Übereinstimmung mit einem ähnlichen Wert, der früher für das westliche Nordatlantische Becken berechnet wurde ($\sigma_t = 27 \cdot 232 \pm 0.008$).

Die bathymetrische Isolation des Karibischen Meeresgebiets (Fig. 1) ist eine solche, daß ein Unterschied in den ozeanographischen charakteristischen Faktoren von denen des offenen Atlantischen Ozeans in einer Tiefe von 1500 m (in beiden Becken, Fig. 2) deutlich festzustellen ist, und dieser Unterschied setzt sich fort die ganze Strecke bis zum Grunde. Was den Sauerstoff betrifft, haben beide

Becken eine geringere Konzentration als der angrenzende Atlantische Ozean; das Cayman-Becken hatte eine größere Konzentration als das Karibische; in 4500 m Tiefe hatte das Cayman-Becken 5.8 ccm pro liter, und das Karibische 5.18 ccm pro liter; das letztere hatte ungefähr 0.9 ccm weniger Sauerstoff pro liter als das Wasser im angrenzenden Atlantik. In beiden Becken stieg der Gehalt an Sauerstoff (unterhalb der Minimumkonzentration) kontinuierlich bis zum Grunde.

Die Sauerstoffverteilung deutet auf bestimmte Möglichkeiten betreffs des Ursprunges des tiefen Wassers im Karibischen Meeresgebiet hin. Diese sind: 1. die verhältnismäßig großen Sauerstoffgehalte beider Becken bilden einen hinreichenden Hinweis dafür, daß die tiefsten Wassermassen ursprünglich an der Oberfläche in hohen Breitegraden gebildet werden, von wo sie diesem Gebiet durch die verschiedenen Passagen zwischen den Inseln zugeführt wurden; 2. der Unterschied im Sauerstoffgehalt zwischen den tieferen Teilen des Karibischen und des Cayman-Beckens kann vielleicht (wenn man dazu die bathymetrischen Verhältnisse in Betracht zieht), darauf hinweisen, daß die tiefsten Teile dieser Becken unabhängig voneinander versorgt werden (das Karibische hauptsächlich durch die Anegada-Passage und das Cayman-Becken durch die Windward-Passage); 3. die Tatsache, daß unter der Schicht der Minimumkonzentration an Sauerstoff der Gehalt an Sauerstoff in beiden Becken (im allgemeinen) abwärts bis zum Grunde ansteigt, könnte einen Beweis dafür darstellen, daß eine Zufuhr von sauerstoffreicherem Wasser am oder nahe dem Grunde stattfindet. Dieser letztere Zustand hat zur Voraussetzung, daß Wasser von etwas größerer Dichte, als man es im Karibischen Becken in der Nähe der Tiefe der Schwelle findet, durch die verschiedenen Passagen einfließt und gleich bis zum Boden sinkt. Der Mechanismus, der eine solche Erneuerung des Wassers zustande bringen könnte, ist nicht bekannt, aber es wird vermutet, daß er mit den kurzperiodischen senkrechten Oszillationen des Meeres verbunden sein könnte.

Printed in Germany

Contribution No. 193

FEBRUARY, 1939 J. O. S. A. VOLUME 29
Printed in U. S. A.

Laboratory Analysis of the Selective Absorption of Light by Sea Water*

George L. Clarke, *Harvard University, Cambridge, Massachusetts*

AND

Harry R. James, *Hastings College, Hastings, Nebraska*

(Received November 25, 1938)

PRECISE laboratory measurements of the absorption of light by distilled water and by samples of water from a large number of Wisconsin lakes have been carried out by James and Birge[1] (1938) using a tube one meter long and a highly sensitive monochromator covering wavelengths 3650–8000A. Opportunity to make use of the same instrument for similar measurements on samples of sea water presented itself during the summer of 1938 as a part of the limnological program of the Wisconsin Geological and Natural History Survey. The authors are indebted to Dr. E. A. Birge and Dr. C. Juday for creating this opportunity and for their help and valuable suggestions throughout the undertaking.†

The purpose of the present investigation was to establish the general form of the absorption curves for specimens of sea water from various typical areas of the ocean and to analyze the different effects of dissolved and suspended material in the waters of the several regions. In the only previous laboratory measurements of sea water, namely those of Hulburt,[2, 3] which were limited to samples from off-shore, and those of Sawyer,[4] which involved coastal water only, an analysis of the sort contemplated was not undertaken. Furthermore, we proposed to compare our absorption values with measurements of light penetration made by lowering a photometer into the water at the same time and place at which our samples were taken. In neither of the former investigations were comparisons made with contemporaneous field measurements.

A special objective in this investigation was to ascertain in what particulars "pure" sea water differs from distilled water in its optical properties. It was proposed to attack this problem by obtaining sea water from the open ocean and removing the particulate matter by passing it through a Berkefeld filter. We define such water as "pure" sea water. The absorption of this water in every part of the spectrum within the range of our instrument may be compared with distilled water. Information would thus be gained as to whether the salts in solution or any other filter-passing material exert an appreciable effect on the general transparency, and particularly whether they have any selective action on light.

A further important object of the present undertaking was to determine to what degree the differences in transparency of various ocean waters are caused by "suspensoids" and to what extent to filter-passing material. Suspensoids are defined as all particulate matter which is removed from the water by a "fine" Berkefeld filter (following James and Birge), and filter-passing material (termed "color" by James and Birge) includes substances in true solution as well as suspended matter too fine to be retained by the filter. This point could be settled by obtaining samples from areas differing sharply in transparency, Berkefeld filtering the water, and then comparing the absorption measurements of the filtrates. Another respect in which oceanic areas differ is in the part of the spectrum to which they are most transparent.[5] The question has always existed as to whether this

---

* From the Woods Hole Oceanographic Institution, Contribution No. 193. From the Limnological Laboratory of the Wisconsin Geological and Natural History Survey. Notes and Reports No. 88.

[1] H. R. James and E. A. Birge, "A Laboratory Study of the Absorption of Light by Lake Waters," Trans. Wis. Acad. of Sci. **31**, 1–154 (1938).

† This investigation was supported by grants from the Wisconsin Alumni Research Foundation, the Brittingham Trust Fund, and the Woods Hole Oceanographic Institution. The authors also wish to acknowledge the assistance of Mr. Dean F. Bumpus in the collection of water samples and the field measurements of light penetration.

[2] E. O. Hulburt, "The Transparency of Ocean Water and the Visibility Curve of the Eye," J. Opt. Soc. Am. and Rev. Sci. Inst. **13**, 553–556 (1926).

[3] E. O. Hulburt, "The Penetration of Ultraviolet Light into Pure Water and Sea Water," J. Opt. Soc. Am. and Rev. Sci. Inst. **17**, 15–22 (1928).

[4] W. R. Sawyer, "The Spectral Absorption of Light by Pure Water and Bay of Fundy Water," Conts. Can. Biol. and Fisheries, n. s. **7**, No. 8, 75–89 (1931).

[5] R. H. Oster and G. L. Clarke, "The Penetration of the Red, Green and Violet Components of Daylight into Atlantic Waters," J. Opt. Soc. Am. **25**, 84–91 (1935).

TABLE I. *Locations from which water samples were obtained.*

SAMPLE NUMBER	STATION NUMBER	LOCATION	LATITUDE	LONGITUDE	DATE COLLECTED 1938	TREATMENT OF WATER AT TIME OF COLLECTION[*]	LIGHT PENETRATION MEASUREMENT SERIES NO.
1	5	Buzzards Bay[‡]	41°33′N.	70°42′25″W.	June 22	Unfiltered	(325)[†]
2	4	Vineyard Sound[§]	41°30′	70°36′	June 22	Unfiltered	(322)[†]
3	3	V. S. Whistle Buoy[‖]	40°17′30″	71°00′	June 25	Unfiltered	
4	3	V. S. Whistle Buoy[‖]	40°17′30″	71°00′	June 25	Unfiltered	
5	C	Sargasso Sea	35°05′	67°06′	July 10	Unfiltered	473
6	C	Sargasso Sea	35°05′	67°06′	July 10	Unfiltered	
7	B	Continental Slope	39°20′	70°33′	July 14	Unfiltered	476
8	B	Continental Slope	39°20′	70°33′	July 14	Paper filtered	
9	A	Continental Shelf	40°38′	71°38′	July 17	Unfiltered	478
10	A	Continental Shelf	40°38′	71°38′	July 17	Paper filtered	
11	3	V. S. Whistle Buoy[¶]	40°17′30″	71°00′	July 29	Unfiltered	480
12	3	V. S. Whistle Buoy[¶]	40°17′30″	71°00′	July 29	Berkefeld filtered	

[*] 10 cc of $HgCl_2$ was added to each carboy at the time of collection.
[†] Measurements made four years previous.
[‡] Tide in Woods Hole running west.
[§] Tide off West Chop running west.
[‖] Tide off Gay Head had run west for one hour.
[¶] Tide off Gay Head running east.

difference is caused entirely by selective scattering by suspensoids or whether filter-passing material may be effective. That part of the selective absorption due to filter-passing material (other than pure water) will be designated as "color." Many lakes have color in this sense and we wished to learn if the same was true of any samples of sea water. If any such color effect were found in sea water, one would expect it to be slight, since no specimens of sea water appear colored to the naked eye as water samples from lakes often do.

COLLECTION OF WATER SAMPLES

The locations from which water samples were collected (see Table I)[*] were chosen so as to cover the entire range of transparencies found in the ocean and at the same time to test water masses which are typical of large portions of the sea. At the four most important stations complete series of measurements of the penetration of daylight were made with a submarine photometer at the same time that the water samples were collected. At the other two locations simultaneous field measurements could not be arranged, but the characteristic transparency of the water at these points is known from earlier observations.

The water was dipped up from the surface in all cases and poured into five-gallon glass carboys. For samples one to ten inclusive, a galvanized bucket and tin funnel were used, but a wooden bucket and glass funnel were employed in the collection of samples 11 and 12. To all samples which were left unfiltered at the time of collection 10 cc $HgCl_2$ per carboy were added immediately. This was necessary in order to prevent bacterial action which otherwise would cause significant changes in transparency within a few hours. Samples 8 and 10 were passed through a paper filter as soon as collected and the preservative added immediately afterwards. The carboy containing the freshly collected sample 12 was placed in the ice box on board ship during the three-hour run to the laboratory. The sample was then passed through a specially prepared "fine" Berkefeld filter[†] and thence directly into another carboy to which the preservative was added. All carboys were landed at Woods Hole and shipped to the University of Wisconsin where the monochromator was in operation.

---

[*] The location of Stations 3, 4 and 5 is shown on the map of Fig. 1, reference 6.

[6] G. L. Clarke, "Seasonal Changes in the Intensity of Submarine Illumination off Woods Hole," Ecology **19**, 89–106 (1938).

[†] A slightly used Berkefeld filter of "fine" porosity was prepared as follows: 5 liters of 10 percent $HgCl_2$ were run through the filter. Then the candle was removed and boiled in 10 percent $NaHCO_3$. The filter was thoroughly rinsed by passing a carboy of distilled water through it. The candle was then dried and the base dipped in paraffin until all metal parts were thoroughly coated inside and out. The apparatus was arranged in such a way that in leaving the filter the water came in contact with nothing but glass. Dust was excluded from the air stream by means of cotton plugs.

LABORATORY MEASUREMENTS OF ABSORPTION

A. Procedure

The arrangement of the apparatus‡ and the procedure in the absorption measurements were the same as those described by James and Birge[1] with the exception of the method of lining the brass tube in which the samples were placed. The silver lining used for certain of the measurements of distilled water was obviously out of the question for sea water. For all of the present measurements the inside of the tube was blackened by treatment with ammoniacal copper carbonate and three different materials were tried for a lining coat. The first of these was paraffin, which had been used in the case of the measurements of lake water. On several occasions the absorption of samples of sea water was found to increase at the blue end of the spectrum as it stood in the tube. The same situation was encountered when the tube was lined with glyptal resin. With a lining of ceresin wax, however, no measurable change in the absorption was found to occur even after the water had stood in the tube over night. But as a precaution our tests were always run immediately after placing the water in the tube, beginning with wave-length 3650A. The measurement at 3650A was repeated at the end of the series.

During the time which had elapsed between the collection of the water and the laboratory measurements particulate matter had settled to the bottom of the carboys. It was obvious that since this material had been in suspension in the water when the field observations were made, its effect on absorption should be included in comparing the laboratory measurements with those made at sea. Accordingly, the carboys were shaken up before the water was poured out into the tube. The probable influence of changes in the physical nature of the suspensoids caused by standing and by the preservative, and the possible reaction of the sea water with the glass of the containers are discussed below.

The majority of measurements on lake water carried out by James and Birge were made with "settled" water rather than "shaken" water and certain tests were run on the sea water samples after they had been allowed to stand. Since the length of time of settling has a very pronounced effect on the absorption value of sea water even after a week—as is also the case with lake water,[7] —a standard period of forty-eight hours after shaking was adopted for settling. The water was then siphoned into the tube and measured immediately.

In addition to the tests run on the freshly shaken water and on settled water, certain samples were subjected to Berkefeld filtering in the Wisconsin laboratory. The Berkefeld filter used for this purpose was also of the "fine" type and was prepared in similar fashion to the one used in Woods Hole. After the discovery of the possible trouble with the paraffin lining of the tube, the paraffin was removed from the base of the filter and the metal parts were recoated with ceresin.

B. Absorption measurements

The measurements of absorption undertaken in the Wisconsin laboratory are presented graphically in Figs. 1–7. The measurements represented by Figs. 1–4 inclusive were carried out toward the end of the work and are the most reliable, since profit was made of earlier experience. All the curves in these figures are based on measurements with the tube lined with ceresin wax.* In all four cases, however, at least one measurement had been completed on another portion of the unfiltered water using the resin-lined tube. Since the two sets of observations are in substantial agreement, they serve as a check on each other and show that the resin lining was sufficiently reliable in cases in which the tests were run immediately. In the case of Station *C* (sample 5) a third portion of the water was run (in ceresin-lined tube) and this agreed well with

---

‡ The effective length of the tube was 97 cm. The accuracy of the measurements was approximately as follows: 5 percent for readings where absorption was more than 10 percent per meter, 10 percent for readings where absorption was between 5 percent and 10 percent per meter, 30 percent for readings where absorption was between 1 percent and 3 percent per meter.

[7] Reference 1, Fig. 19.

* The tube used was slightly less than 1 meter longer than the comparison tube (see reference 1), hence the absorption values given are too low for 1 m by a small amount. Since the correction for these relatively transparent waters is so slight (maximum = 1 percent at 7600A) and becomes less than 0.1 percent at all wave-lengths shorter than 7400A, it has been neglected.

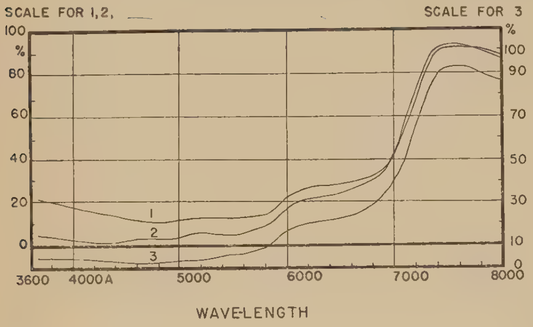


FIG. 1. Sargasso water. Station *C*. Percentage absorption of light per meter. Curve 1—sample 5, not filtered when collected, measured August 10, 1938, after shaking. Curve 2—sample 5, not filtered when collected, measured August 11, 1938, after Berkefeld filtering. Curve 3—double-distilled water, measured in ceresin-lined tube. (Curve displaced downward by 10 units to avoid interference.)

the second. Such differences as did occur between duplicate observations were confined to the short wave-length end of the spectrum and were particularly noticeable at 3650A. This situation can be accounted for in part by the fact that measurements are less precise in this region (because of the smaller amount of energy emitted by the source and the extremely high transparency of the water here) and in part by the fact that the absorption of water itself is so high at longer wave-lengths that the effect of other substances is masked. Insofar as any foreign matter present causes an increase in scattering (as distinct from true absorption), one would expect a greater effect toward the short wave-length end of the spectrum.

The absorption of those samples of water from Stations *C*, *B*, *A* and 3 which were not filtered at the time of collection was first measured immediately after moderate shaking (curve 1, in Figs. 1–4). Following this in each case the water was run out of the tube, passed through the Berkefeld filter, and then measured again (curve 2). These two measurements may be compared with doubled-distilled water† (curve 3) tested in the same tube under identical conditions. At Station *C* a second sample (sample 6) was collected in the same way as the first, but its absorption was found to be very much greater (Table II). Since the sample appeared perceptibly milky as it stood in the carboy, it was obvious that contamination of some sort had taken place. Although Berkefeld filtering reduced the absorption of this water to a minimum of 1.7 percent at 5040A, the value at 3650A is seen to be very much higher than that for the first Station *C* sample (sample 5). Much of the foreign matter present was therefore either in solution or in the form of very small particles.

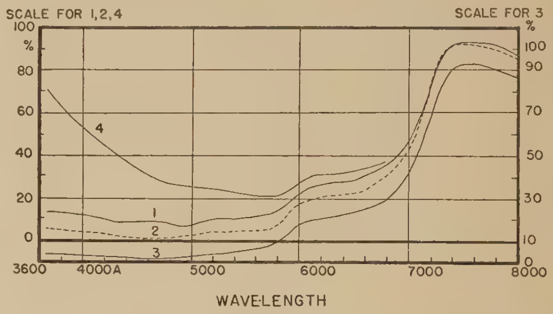


FIG. 2. Continental Slope water. Station *B*. Percentage absorption of light per meter. Curve 1—sample 7, not filtered when collected, measured August 12, 1938, after shaking. Curve 2—sample 7, not filtered when collected, measured August 12, 1938, after Berkefeld filtering. Curve 3—double-distilled water measured in ceresin-lined tube. Curve 4—sample 8, paper filtered when collected, measured August 10, 1938, after shaking.

The absorption measurements of those samples of sea water which were filtered at the time of collection (curve 4, Figs. 2–4), may be compared with the foregoing cases. Contrary to expectation, samples 8 and 10 (from Stations *B* and *A*), which were paper filtered, exhibited a greatly increased absorption in the short wave-length part of the spectrum. Since both samples behaved in the same way, one supposes that the water picked up a large amount of material from the filter paper. No further study of these samples seemed worthwhile.

The curve for the second sample at Station 3 (sample 12), which was Berkefeld filtered at the time of collection, is closely similar in shape to that for the first sample (sample 11), which was filtered in the Wisconsin laboratory, although the former lies somewhat above the latter at the shorter wave-lengths. After this initial measurement, sample 12 was Berkefeld filtered again, this time in the Wisconsin laboratory. Since the absorption remained unchanged, we have proof that the Berkefeld filter used at Wisconsin did not affect appreciably the absorption characteristics of sea water. It is possible that the filter used in Woods Hole added "color" to the water since the absorption in the blue region of the spectrum was higher for sample 12 than for sample 11 after Berkefeld filtering. The difference is so slight, however, that it may well be caused by a difference in the two original samples. The fact that sample 11 has a lower absorption strongly indicates that no colored material dissolved out of the particles present in this sample during the period between collection off Woods Hole and filtering at Wisconsin (thirteen days). An average between curves 2 and 4 (Fig. 4) would therefore give a reliable picture of the absorption of Station 3 water with suspensoids removed.

---

† Distilled water redistilled in a tin still and run into Pyrex glass container. The absorption measurements were carried out on the same day. A second portion of the water prepared in this way agreed as well as could be expected with the first (cf. reference 1). The absorption curve of this sample was not appreciably changed by passing it through the same Berkefeld filter. Proof was thus furnished that the filtering process does not add "color" or otherwise affect the water itself.

The samples collected earlier (samples 1–4) from locations near shore (Station 3, 4 and 5) may be considered briefly (Figs. 5–7). Although the absorption of these samples was measured in the paraffin-lined tube, some reliance can evidently be placed on these observations since the curve for sample 4, Station 3, for shaken water (curve 1, Fig. 5) agrees fairly well with the corresponding curve for sample 11 (curve 1, Fig. 4) taken five weeks later at the same station and run under more precise circumstances.

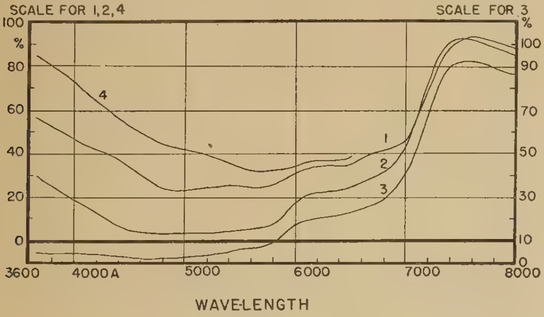


FIG. 3. Continental Shelf water. Station *A*. Percentage absorption of light per meter. Curve 1—sample 9, not filtered when collected, measured August 13, 1938, after shaking. Curve 2—sample 9, not filtered when collected, measured August 13, 1938, after Berkefeld filtering. Curve 3—double-distilled water measured in ceresin-lined tube. Curve 4—sample 10, paper filtered when collected, measured August 11, 1938, after shaking.

After settling for forty-eight hours, the transparency of the samples from all three stations was considerably increased. The greatest difference between shaken and settled water was found in the case of the sample from Vineyard Sound (Station 4). Since this is the most turbulent of the localities sampled, it may be that the particles present in this case were heavier and hence would settle out faster. The settling process resulted in reduction of absorption throughout the spectrum and the effect was generally uniform between wave-lengths 4000 and 7000A. Above 7000A the high absorption of water itself largely obscures the effect of other material; below 4000A the effect of filter-passing material appears, as will be discussed below. We conclude that the effect of particles large enough to settle out within forty-eight hours is nonselective within this central part of the spectrum.

C. Artificial sea water

An attempt to test the effect of the principal salts of sea water on absorption was made by preparing an artificial sea water and comparing it with distilled water. Four gallons of double-distilled water were prepared and divided into two parts. To one part the following salts were added in the proportions indicated (same formula as used by Hulburt[3]):

NaCl	26.40 g
KCl	.75
$MgCl_2$	3.15
$MgSO_4$	2.07
$CaSO_4$	1.33
	33.70
H_2O	966.30
	1000.00 g

All salts were of "reagent quality" with the exception of the $CaSO_4$ which was Mallinckrodt "pure precipitated." Due allowance was made for the water of crystallization. Since $MgCl_2$ is highly hygroscopic, some water was unavoidably included, with the result that the amount of this salt was probably slightly too small. The solution was thoroughly shaken and allowed to stand for two days. At the end of this time the water was not perfectly clear to the naked eye, but contained very fine particles—whether of undissolved salts or of impurities could not be determined. After Berkefeld filtering the solution was clear and its absorption was measured the following day. The second portion of double-distilled water was similarly passed through the

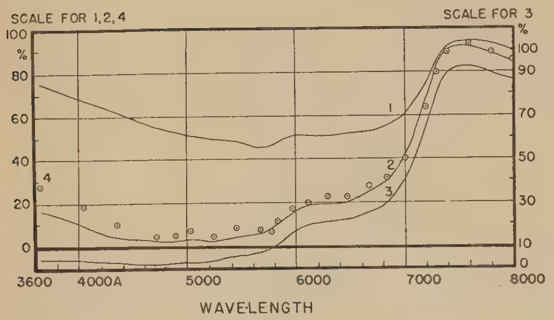


FIG. 4. Vineyard Sound Whistle Buoy. Station 3. Percentage absorption of light per meter. Curve 1—sample 11, not filtered when collected, measured August 11, 1938, after shaking. Curve 2—sample 11, not filtered when collected, measured August 11, 1938, after Berkefeld filtering. Curve 3—double-distilled water measured in ceresin-lined tube. Curve 4—sample 12, Berkefeld filtered when collected, measured August 9, 1938, after shaking.

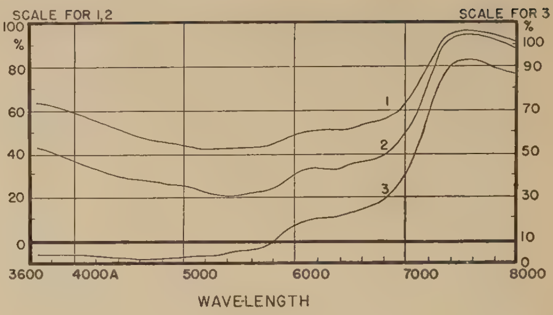


FIG. 5. Vineyard Sound Whistle Buoy. Station 3. Percentage absorption of light per meter. Curve 1—sample 4, not filtered when collected, measured July 6, 1938, after shaking. Curve 2—sample 4, not filtered when collected, measured July 6, 1938, after settling 48 hours. Curve 3—double-distilled water measured in ceresin-lined tube.

Berkefeld filter and a comparative measurement made (Fig. 8).

The absorption of the artificial sea water is seen to be practically identical with the double-distilled water from 8000A to 5460A. At shorter wave-lengths the artificial sea water exhibits a higher absorption, especially at 3650A. This effect is probably caused chiefly, if not entirely, by filter-passing impurities and not to the salts in solution, because our clearest samples taken from the ocean and Berkefeld filtered, which contain the same salts, exhibited an absorption only slightly greater than distilled water (cf. curves 2, Figs. 1 and 2). Hulburt[3] similarly concluded that the salts of sea water exerted no appreciable effect on absorption at wave-lengths longer than 3400A. Furthermore, we obtain no evidence from these measurements that the presence of these salts in sea water could reduce the absorption below that of distilled water. The significance of this conclusion will appear below in the discussion.

TABLE II. *Comparison of absorption per meter of samples 5 and 6 at five wave-lengths. Both samples were taken at Station C. Neither was filtered at the time of collection, but sample 6 had evidently become contaminated.*

Wave-Length	Water Freshly Shaken		Water Berkefeld Filtered	
	Sample 5	Sample 6	Sample 5	Sample 6
5790A	14.0%	48.8%	7.2%	8.4%
5460	13.6	47.3	4.3	6.2
4359	15.1	61.9	1.0	10.0
4047	17.8	69.1	2.8	16.7
3650	22.5	72.5	5.4	27.8

OBSERVATIONS AT SEA

The measurements at sea were made according to our usual procedure and in close conformity to the recommendations of the Committee of the International Council for the Exploration of the Sea.[8] Our submarine photometer and deck photometer contain Weston "Photronic" cells which possess a maximum spectral sensitivity at 5800A.[9] For the present measurements a Schott-Jena filter, type VG-2 (practically identical to the VG-9 recommended by the Committee) was placed between the plate glass window of the photometer case and the opal glass diffusing disk.* The transmission of this filter reaches a maximum at 5300A and drops off to 10 percent of the maximum at about 6200A and 4600A. The point of maximum sensitivity of the combination of cell plus filter can safely be taken as 5500A.

The observations at sea at Stations *C*, *B*, *A* and 3 are presented graphically in Fig. 9. Since the curves, plotted on a logarithmic scale, approach a straight line, we know that the water

---

[8] A. Angstrom, W. R. G. Atkins, G. L. Clarke, H. Pettersson, H. H. Poole and C. L. Utterback, 1938, "Measurements of Submarine Daylight," J. du Conseil Perm. Intern. pour l'Exp. de la Mer **13**, 37–57 (1938).

[9] Weston Electrical Instrument Corporation Technical Data Pamphlet.

* For high light intensities a diaphragm was placed over this disk to reduce the illumination. Both photometers were carefully calibrated against a photoelectric cell which was known to be linear in its response (Powell and Clarke, reference 10).

[10] W. M. Powell and G. L. Clarke, "The Reflection and Absorption of Daylight at the Surface of the Ocean," J. Opt. Soc. Am. **26**, 111–120 (1936).

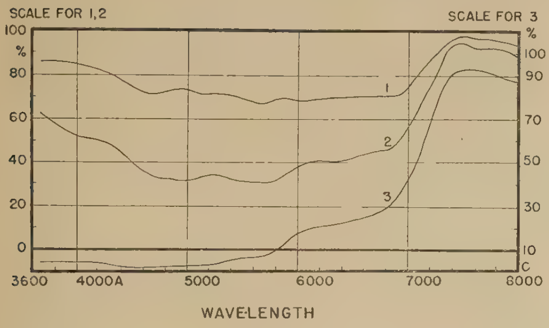


FIG. 6. Vineyard Sound water. Station 4. Percentage absorption of light per meter. Curve 1—sample 2, not filtered when collected, measured July 7, 1938, after shaking. Curve 2—sample 2, not filtered when collected, measured July 7, 1938, after settling 48 hours. Curve 3—double-distilled water measured in ceresin-lined tube.

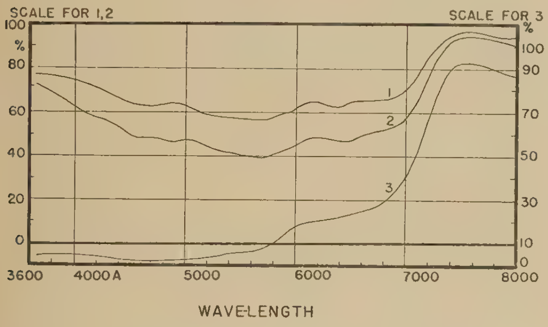


FIG. 7. Buzzards Bay water. Station 5. Percentage absorption of light per meter. Curve 1—sample 1, not filtered when collected, measured July 5, 1938, after shaking. Curve 2—sample 1, not filtered when collected, measured July 7, 1938, after settling 48 hours. Curve 3—double-distilled water measured in ceresin-lined tube.

was homogeneous optically.† The calculation of *average* values for the extinction coefficient‡ and for the percentage absorption for water is therefore appropriate (Table III). The values obtained are in close conformity to previous observations[11] in the several regions and demonstrate the presence of the clearest water in the Sargasso Sea (Station *C*). Water of progressively lower transparency was encountered in the Continental Slope area (Station *B*) and on the Continental Shelf (Station *A*). The extinction coefficient characterizing the water at the whistle buoy at the western entrance to Vineyard Sound (Station 3) was nearly the same as at Station *A* and falls within the narrow range of values previously obtained for Station 3 during the summer months.[6] Thus at all four stations the transparency of the sea at the time of collection of the water samples for laboratory measurements was shown to be entirely typical of the respective regions.

For field measurements at Stations 4 and 5 (Vineyard Sound and Buzzards Bay) we have the observations of Oster and Clarke[5] made on August 21 and August 28, 1934, respectively (Series 322 and 325), with instruments of almost identical spectral sensitivity and under similar conditions of tide (Table III). These measurements and others placed the transparency of Buzzards Bay somewhat below that found within Vineyard Sound and this in turn was considerably below that observed at the entrance to the Sound (Station 3).

Since the water samples for laboratory measurement were collected at the surface, one might suppose that their absorption values should be compared with field measurements made just beneath the surface. However, it is ordinarily impossible to carry out reliable field measurements at depths of less than one or two meters Furthermore, when the curves representing the measurements at greater depths (Fig. 9) are extended upwards from the shallowest point of observation to the surface, they do not strike the 0–m line at 100 percent, but at a lower value

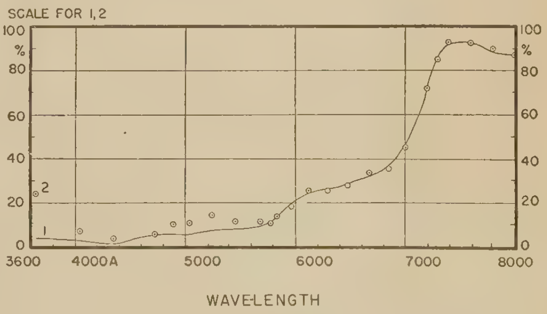


FIG. 8. Curve 1—percentage absorption per meter of one portion of double-distilled water after Berkefeld filtering. Curve 2—percentage absorption per meter of artificial sea water (see text) made from a second portion of the double-distilled water and passed through the Berkefeld filter.

---

† The decreased transparency indicated below 25 m at Station 3 (Series 480) is probably a result of mud stirred up from the bottom (depth 31 m).

‡ Extinction coefficient $=k$ in the equation $I/I_0=e^{-kL}$ where L is the thickness of the water layer (in meters) in which the intensity is reduced from I_0 to I. The term "transmissive exponent" was formerly used for this quantity following Sawyer, reference 4, but has been changed to conform to the recommendations of the Committee (reference 8). "Absorption coefficient" has been used by certain other investigators in the same connection.

[11] G. L. Clarke, "Light Penetration in the Western North Atlantic and its Application to Biological Problems," Rapports et Procès-Verbaux. Con. Perm. Intern. Exp. Mer. **101**, Part 2, 3–14 (1936).

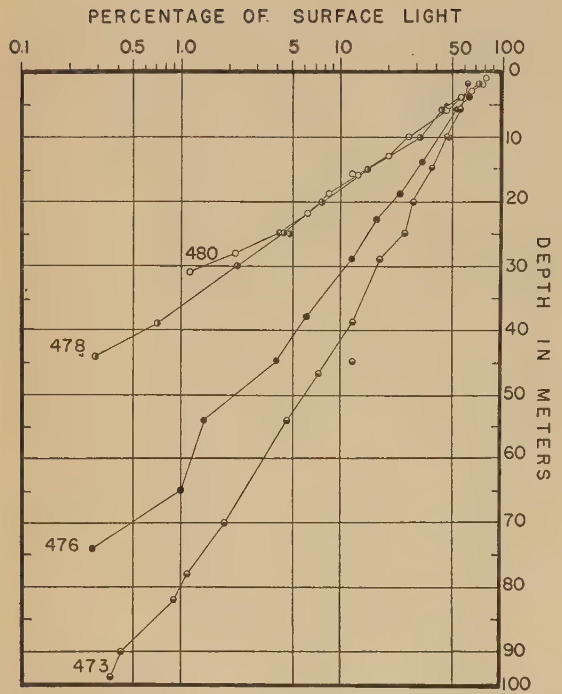


FIG. 9. Measurements of light absorption carried out at sea. Curves show relation between depth and illumination expressed as a percentage of the light just over the surface (logarithmic scale). Maximum sensitivity of photometer 5500A (photronic cell with VG-2 filter). Series number indicated at end of each curve (see Table I for additional data).

SERIES	LOCALITY	STATION	DATE	TIME (E.S.T.)	SKY	SEA	WIND
473	Sargasso Sea	C (3093)	July 10, 1938	11:37–12:13	*bc*	2	2
476	Continental Slope	B (3105)	July 14, 1938	12:47–13:30	*b*	5	5
478	Continental Shelf	A (3111)	July 17, 1938	11:46–12:10	fog	1	1
480	Vineyard Sound Whistle Buoy	3	July 29, 1938	11:50–12:30	*o*	2–3	2–3

ranging down to 70 percent in the present case. This effect, termed the "surface loss," has been shown to be caused in only a small degree by actual reflection at the surface. The greater part of the "loss" is accounted for by the greatly increased absorption of the water layer (about one meter thick) just beneath the surface (probably caused by bubbles) under all conditions except absolute calm.[10] Obviously this situation within the upper meter is a local and temporary effect yielding an extinction value not inherent in the water itself. Since the ocean water in the regions under consideration is thoroughly stirred down to at least 25 m, an average value for the absorption over this depth has been taken for comparison with the laboratory measurements (Table III).

DISCUSSION

A. Comparison of laboratory measurements with observations at sea

If the same picture of submarine illumination is obtained from the extrapolation of laboratory measurements of absorption as is derived from actual observations at sea, work on board ship would be greatly simplified and measurements could be carried out under ideal conditions on shore. A comparison of the curves for the shaken samples from all the stations (Fig. 10) shows that the transparencies of the samples follow the same general sequence as that based on measurements at sea. There are two exceptions: The sample from the Continental Slope (Station *B*) exhibited less absorption than that from the Sargasso Sea (Station *A*), and the sample from Buzzards Bay (Station 5) was less opaque than that from Vineyard Sound (Station 4).

For the comparison of absolute values we may take the absorption observed in the laboratory for wave-length 5500A since this is the region of maximum sensitivity of the photometer used at sea (see above). It is seen that the absorption per meter as measured in the laboratory is from 2 to 4 times greater than the absorption based on the field measurements (Table III). Higher absorption is likewise found even if the minimum value for each curve at any wave-length is taken. The water was evidently considerably changed by the time it reached the Wisconsin laboratory. This situation was anticipated because according to common experience any semi-transparent organic tissue present would be rendered opaque by the preservative. In addition, the water may have reacted with the glass of its containers. If the latter explanation was operative, its effect must have been small since we have one unfiltered sample (sample 7) in which the absorption was very little above distilled water and the action of the sea water would be expected to be the same in all cases. Furthermore, after Berkefeld filtration, the absorption of samples 5 and 7 was reduced practically to that of distilled water although the samples had stood in their containers for over a month. It seems more likely that the transparency of suspended particles had become radically altered. Such action of the preservative on *different types* of organic matter would account for the differences in amount of change undergone by the various samples. For example, the transparency of the water at Station *A* was closely similar to that at Station 3 as measured at sea, but an absorption of twice the magnitude was obtained for the latter station from the laboratory samples. The conclusion is obvious that much though we may learn from laboratory studies of light absorption, they cannot give a reliable picture of the illumination actually to be found at various depths in the ocean. For this, observations at sea are essential.

B. Comparison of "pure" sea water with distilled water

The absorption of "pure" sea water, as represented by samples taken from the off-shore stations (Stations *B* and *C*) and passed through the Berkefeld filter, was found to be practically identical with the ordinary double-distilled water measured in the ceresin-lined tube within the variation of measurement (Table IV). The absorption values for the best samples of distilled water measured in a silver lined tube[1] are somewhat lower than for sea water. It is of interest to note that our values for the absorption of both of these samples of sea water at wave-lengths 4047A and 3650A are lower than those of Sawyer[4] for distilled water, the difference being about fourfold at 3650A (Table V). (They are also lower than the values reported by Hulburt[3] for distilled water and for sea water at 3660A and the value of Dawson and Hulburt[12] for distilled water at 3600A.) This fact adds strong support to the evidence from the distilled water measurements of James and Birge that Sawyer's values for distilled water in this part of the spectrum are too high. In addition field measurements made in the Sargasso Sea of absorption in the blue region[13] and in the violet region[5] agree closely with our present laboratory measurements and yield values lower than those of Sawyer for distilled water in the corresponding parts of the spectrum (Table V). At the time the discrepancies were assigned to inaccuracies unavoidable in work at sea, but now our laboratory measurements have confirmed the earlier field observations, and both are consistent with the values for distilled water obtained by James and Birge.

Darby, Johnson and Barnes[14] have reported a

---

[12] L. H. Dawson and E. O. Hulburt, "The Absorption of Ultraviolet and Visible Light by Water," J. Opt. Soc. Am. **24**, 175–177 (1934).

[13] G. L. Clarke, "Observations on the Penetration of Daylight into Mid-Atlantic and Coastal Waters," Biol. Bull. **65**, 2, 317–337 (1933).

[14] H. H. Darby, E. R. F. Johnson and G. W. Barnes, "Studies on the Absorption and Scattering of Solar Radiation by the Sea. Spectrographic and Photoelectric Measurements," Carnegie Inst. of Wash. Publication, No. 475, 191–205 (1937).

TABLE III. *Summary of the measurements of the penetration of the "green" component of daylight into the sea and comparison with laboratory measurements of absorption of unfiltered samples taken from the same stations.*

STATION	LOCATION	SERIES NUMBER	RANGE OF MEASUREMENTS	AV. EXTINCTION COEFFICIENT, *k*, OVER RANGE IN PREVIOUS COL.	AVERAGE ABSORPTION PER METER FOR SEA MEASUREMENT	SAMPLE NUMBER	ABSORPTION PER METER AT 5500A FOR SAMPLE IN LABORATORY	MINIMUM ABSORPTION PER METER FOR LAB. SAMPLE	WAVE-LENGTH AT WHICH MINIMUM ABSORP. IS FOUND
			METERS	*k*	%		%	%	A
C	Sargasso Sea	473	2–94	0.056					
			2–25	.040	3.9	5	13	10	4900
B	Continental Slope	476	4–74	.062					
			4–23	.061	5.7	7	10	7	4900
A	Continental Shelf	478	2–44	.13					
			2–25	.12	11.3	9	26	22	4900
3	V. S. Whistle Buoy	480	1–31	.14					
			1–25	.125	11.7	{11	48	45	5790 and 5685
						4	43	42	5250
4	Vineyard Sound	322	1–21	.20	18.1	2	69	67	5685
5	Buzzards Bay	325	1–15	.25	22.1	1	57	57	5685

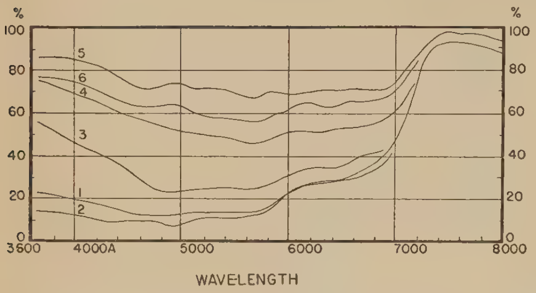


FIG. 10. Comparison of percentage absorption of light per meter for unfiltered samples of sea water from all stations measured after shaking.

CURVE	LOCALITY	STATION	SAMPLE
1	Sargasso Sea	*C*	5
2	Continental Slope	*B*	7
3	Continental Shelf	*A*	9
4	Vineyard Sound Whistle Buoy	3	11
5	Vineyard Sound	4	2
6	Buzzards Bay	5	1

very much lower rate of absorption for ultraviolet by sea water on the basis of field measurements near the Tortugas Laboratory (Gulf of Mexico) than found by Sawyer and by Hulburt. Since the work of Darby *et al.* yielded only relative values, comparisons with other measurements are difficult. Since field measurements by Clarke[15] in the visible part of the spectrum gave very low values for the extinction coefficient in the Gulf of Mexico, there is no doubt that the water in this region is extremely transparent. But whether the penetration of the far ultraviolet is as effective as suggested by Darby *et al.* remains to be confirmed. The determination of absolute values in this biologically important region of the spectrum is seriously needed. Certainly the low absorption values as far as 3650A obtained in the present investigation lend support to the view that ultraviolet is not reduced in intensity by sea water as rapidly as was previously supposed.

As regards the long wave-length end of the spectrum, our measurements show that the values for *k* of 0.567 and 0.480 for sea water at 7600A and at 7000A, respectively, reported by Atkins and Poole[16] are far too low. Atkins[17] believes the explanation to lie in erroneous ratings of the average wave-lengths transmitted by the combinations of filters used by him. The table of "accepted values" for the extinction coefficients of distilled water given by Cooper and Milne[18] is consequently seriously in error. Since there is no reason to suppose that the transparency of sea water can ever exceed that of distilled water, we must conclude that the measurements of James and Birge give a truer description of distilled water than those of earlier investigators. Furthermore, our present investigation shows that "pure" sea water approaches the transparency of distilled water *as reported by James and Birge* in all parts of the spectrum.

C. The effect of suspensoids and of filter-passing material on absorption

Since Berkefeld filtering sea water from Station 3 after a period of storage (sample 11) had es-

TABLE IV. *Comparison of "pure" sea water with distilled water. Percent absorption per meter.*

	BERKEFELD-FILTERED SEA WATER		DISTILLED WATER	
WAVE-LENGTH	STATION B SAMPLE 7†	STATION C SAMPLE 5†	CERESIN-LINED TUBE	SILVER-LINED TUBE*
8000	85.2	86.6	86.8	88.9
7800	89.0	89.7	89.5	90.2
7600	91.6	92.2	92.3	91.4
7400	91.5	91.2	89.5	88.5
7300	85.0	84.5	80.5	
7200	71.0	69.8	65.5	64.5
7000	42.7	42.2	39.3	45.0
6850	32.3	31.8	29.7	38.0
6680	28.7	28.3	28.6	33.0
6480	22.0	24.4	22.8	28.0
6300	20.6	22.3	21.0	25.0
6125	19.7	21.2	19.9	22.4
5970	16.6	15.2	16.2	17.8
5840	8.2	9.6	9.1	9.5
5790	7.6	7.2	8.9	
5685	5.0	7.4		4.6
5460	4.8	4.2	6.5	3.8
5250	4.1	6.2	3.9	1.8
5040	2.6	4.5	4.0	1.0
4900	1.7	2.8	2.2	
4730	1.0	3.6	1.7	0.49
4480				0.70
4359	2.8	1.0	2.3	0.78
4047	4.4	2.8	4.1	1.1
3650	6.6	5.4	4.5	3.6

* From James and Birge, 1938, Table I.
† Ceresin-lined tube.

---

[15] G. L. Clarke, "Light Penetration in the Caribbean Sea and in the Gulf of Mexico," J. of Marine Research **1**, 85–94 (1938).

[16] W. R. G. Atkins and H. H. Poole, "The Photo-electric Measurement of the Penetration of Light of Various Wave-Lengths into the Sea and the Physiological Bearing of the Results," Phil. Trans. Roy. Soc. London. **B222**, 129–164 (1933).

[17] Private communication.

[18] L. H. N. Cooper and A. Milne, 1938. "The Ecology of the Tamar Estuary. II. Under-Water Illumination," J. Mar. Biol. Ass. **22**, 509–528.

TABLE V. *Comparison of field measurements of light absorption in the blue and violet regions with laboratory measurements of sea water and of distilled water.*

FIELD MEASUREMENTS IN SARGASSO SEA						LABORATORY MEASUREMENTS				
							FILTERED SEA WATER		DISTILLED WATER	
	MAX. SENSITIVITY OF PHOTOMETER	AV. ABSORPTION FOR WHOLE SERIES		MIN. ABSORPTION FOR 10 m STRATUM		WAVE-LENGTH	STATION *B*	STATION *C*	SAWYER	JAMES AND BIRGE
SERIES	A	*k*	% per m	*k*	% per m	A	% per m	% per m	% per m	% per m
12*	4359	0.031	3.1	0.011	1.1	4359	2.8	1.0	2.6	0.78
						4047	4.4	2.8	6.0	1.3
310†	3650	0.048	4.8	0.022	2.2	3650	6.6	5.4	21.6	3.6

* Reported by Clarke (1933).
† Reported by Oster and Clarke (1935).

sentially the same effect on absorption as immediate filtration (sample 12), we may assume in the case of this and of all the other samples that no significant amount of absorbing material dissolved out of the particles occurring in the water during the period of storage. The filtration process naturally exerted a greater effect on absorption in the case of samples from coastal regions (Stations *A* and 3)* than on samples from off-shore (Stations *B* and *C*) since the former were more turbid initially. The significant fact is that for all four stations Berkefeld filtering reduced the absorption practically to distilled water values for wave-lengths between 8000A and 4730A. The agreement between all curves of filtrates and distilled water is remarkably close (curves 2 and 3, Figs. 1–4). Proof is thereby furnished that between 8000A and 4730A the greater absorption brought about by sea water than by distilled water is entirely caused by suspensoids, i.e., to particles large enough to be removed by the Berkefeld filter.

For the spectral region from 4730A to 3650A suspensoids similarly appear to account for all of the absorption *in the case of samples from the off-shore stations* with the possible exception of the shortest wave-lengths. It is doubtful whether the slightly higher position of the filtrate curves is more than would be accounted for by the variation in measurement. In the case of the inshore samples, however, although the absorption was greatly reduced by filtering in all parts of the spectrum, the curves remain far above distilled water at the short wave-lengths after the samples had been passed through the Berkefeld (curves 2 and 3, Figs. 3 and 4). This fact demonstrates the presence of significant quantities of filter-passing material which has a pronounced absorptive action on light. This material may consist of particles of extremely small size (practically all bacteria are stopped by the Berkefeld filter—cf. Clarke and Gellis[19]) or of substances in true solution.† We may well imagine that material of both kinds would result from the decomposition of plankton, which is much more abundant in coast regions than offshore, and of littoral organisms. Soluble pigments derived from disintegrating plant cells might account for selective absorption (cf. Kalle[20]). In addition discrete particles as small as is indicated would have a highly selective effect on the scattering of light.

The absorption of settled lake waters has been assigned numerically to (1) water as water, (2) "suspensoids," (3) "color" by James and Birge

---

* The samples from the other coastal stations were not Berkefeld filtered.

[19] G. L. Clarke and S. S. Gellis, 1935. "The Nutrition of Copepods in Relation to the Food-Cycle of the Sea," Biol. Bull. **68**, 231–246 (1935).

† Our present method gave no possibility of distinguishing between these two elements; the matter presents a problem for future investigation. It has recently been found that the residual color of many lake waters can be removed entirely or in part by the use of a Cellophane filter (Juday, unpublished communication).

[20] K. Kalle, "Zum Problem des Meereswasserfarbe. Annalen der Hydrographie und Maritimen meteorologie," Heft. I, 1–13 (1938).

TABLE VI. *Percentage transmitted by filter-passing material = C ("color"), and by filter-retained material = S ("suspensoids"), in reducing the transmission of distilled water = W to that observed for the shaken sample = N (see text).*

Wave-Length	Double-Distilled Water	Vineyard Sound Whistle Buoy Station 3 Sample 11					Continental Slope Water Station *B* Sample 7				
	W	*N*	*Fi**	*F = N/W*	*C = Fi/W*	*S = F/C*	*N*	*Fi**	*F = N/W*	*C = Fi/W*	*S = F/C*
8000	13.2	9.8	14.7	74	111†	67	13.6	14.8	103	112†	92.0
7600	7.7	5.6	7.9	73	103	71	7.4	8.4	96.2	109	88.3
7200	34.5	24.8	31.0	72	90†	80	28.0	29.0	81.1	84.2†	96.3
7000	60.7	39.8	59.9	65	99	66	54.1	57.3	89.0	94.4	94.4
6680	71.4	46.3	73.0	65	102	64	67.6	71.3	94.7	100	94.7
6300	79.0	49.0	80.2	62	101	61	72.6	79.4	91.9	100	91.9
5970	83.8	49.9	85.6	60	102	59	79.2	83.4	94.6	100	94.6
5790	91.1	51.9	91.3	57	100	57	87.5	92.4	96.0	101	95.1
5460	93.0	51.1	95.5	54	101	53	89.8	95.1	96.6	102	94.6
5040	96.0	49.0	96.7	51	101	51	91.7	97.4	95.6	101	94.6
4730	98.3	44.8	97.1	46	98.8	47	90.6	99.0	92.2	101	91.6
4359	97.7	38.6	96.6	40	98.8	41	91.3	97.2	93.4	99.5	93.9
4047	95.9	32.6	90.0	34	93.9	36	88.0	95.6	91.8	99.7	92.1
3650	95.5	25.1	83.6	26	87.6	30	86.2	93.4	90.3	97.9	92.2

* *Fi* = transmission of filtered sample. All measurements made in ceresin-lined tube.
† Departure from 100 percent probably due to variation of measurement as indicated by other series of observations.

on the basis of a three-component analysis. The absorption of the water itself is based on the distilled water curve. A similar analysis (Table VI) has been carried out on the two samples of sea water which exhibited the greatest and the least effect resulting from Berkefeld filtering, but in the present case the analysis is based on the shaken water rather than on the settled water for reasons stated above. The factors involved are derived as follows:

N = percentage transmission of shaken sea water*
W = " " " distilled water
Fi = " " " Berkefeld-filtered sea water

$$\frac{N}{W}=F=\text{general factor}$$

$$\frac{Fi}{W}=C=\text{color factor}$$

$$\frac{F}{C}=S=\text{suspensoid factor}$$

$$\therefore CSW=N.$$

The foregoing method of analysis allows one to calculate the part played respectively by suspensoids and by "color" at any desired wave-length in reducing the transmission of pure water to that of the sample under investigation. For example, in the case of off-shore water (sample 7, Station *B*, Table VI) suspensoids reduced the transmission to about 93 percent of that of distilled water with very little difference in any part of the spectrum. Practically no "color" was present since the factor for the transmission allowed by this component does not depart significantly from 100 percent (if questionable values at the long wave-length are disregarded) with the possible exception of wave-length 3650A. In the case of coastal water (sample 11, Station 3) suspensoids account for the reduction of light to values varying from 30 percent at 3650A to 70 percent or 80 percent at the long wave-lengths. Here the effect of suspensoids is considerable throughout the spectrum, but greatest at the shorter wave-lengths. It must be remembered, however, that we have evidence that the transparency of the suspensoids has been seriously changed by the preservative: the factor for suspensoids for *fresh* sea water would be smaller.* The "color" factor for coastal water departs slightly from 100 percent at certain long wave-lengths, but other series of observations show that this is caused by variation of measurement. At the short wave-length end of the spectrum, however, the pronounced selective action of this factor is clearly indicated. Coastal sea water thus possesses some "color" not removable by a Berkefeld filter. We conclude, in sum, that a distinct optical difference exists between off-shore and coastal water: In the former the absorption, beyond that of the water itself, is caused chiefly by suspensoids and these are largely nonselective in their effect on light. In the latter the greater absorption is due to filter-passing material as well as to suspensoids and each of these elements exerts a highly selective action on light.

---

* The symbol "*T*" is used for the transmission of settled water by James and Birge.

* There is no evidence that the preservative affects appreciably the filter-passing material, but this point should be checked when opportunity arises.

Summary

(1) The absorption of light by preserved samples of sea water collected at coastal and at off-shore stations in the North Atlantic was measured in the monochromater previously employed by James and Birge.[1] One sample from each station was left unfiltered at the time of collection and was measured (a) after moderate shaking, (b) after settling for forty-eight hours, and (c) after Berkefeld filtering. Other samples were passed through paper or Berkefeld filters at the time of collection.

(2) Artificial sea water exhibited an absorption practically identical with distilled water except at the shorter wave-lengths where the absorption was greater probably because of impurities.

(3) The absorption per meter of the shaken samples was much greater than the average value per meter for the absorption observed at sea. This fact, undoubtedly caused by the action of the preservative on organic particles, demonstrates the necessity of field observations for an accurate knowledge of submarine illumination.

(4) The absorption of "pure" sea water, as represented by Berkefeld-filtered off-shore samples, was found to be practically identical with distilled water measured in the same tube. Thus no support is furnished to previous reports by others of lower absorption and additional evidence is obtained that the values of Sawyer[4] for distilled water in the ultraviolet may be too high.

(5) The difference between the absorption of unfiltered samples of sea water and of distilled water is caused chiefly by suspensoids for wave-lengths 8000A to 4730A, and for 4730A to 3650A in the off-shore areas. In coastal areas both filter-passing material and suspensoids are effective and each exerts a highly selective action on light with greatest absorption at the shorter wave-lengths.

Contribution No. 194

Memoirs of the Museum of Comparative Zoölogy
AT HARVARD COLLEGE
VOL. LIV. No. 4

STUDIES OF THE WATERS OF THE CONTINENTAL SHELF, CAPE COD TO CHESAPEAKE BAY

III

A VOLUMETRIC STUDY OF THE ZOOPLANKTON

BY

HENRY B. BIGELOW AND MARY SEARS

CAMBRIDGE, U. S. A.
Printed for the Museum
1939

STUDIES OF THE WATERS OF THE CONTINENTAL SHELF, CAPE COD TO CHESAPEAKE BAY. III.[1] A VOLUMETRIC STUDY OF THE ZOOPLANKTON

By Henry B. Bigelow and Mary Sears

Contribution No. 194
From the Woods Hole Oceanographic Institution

---

[1] Parts I and II appeared in Papers in Physical Oceanography and Meteorology, Vol. II, No. 4, 1933 and Vol. IV. No. 1, 1935.

CONTENTS

Page
Introduction 189
  Acknowledgments 190
Geographic limits and subdivisions of the area 190
History and sources of information 190
Methods 192
  Collection 192
  Measurements and calculations 193
  Expression of results 196
Validity of calculated results 197
Part I. The volume of zooplankton 200
  The water column as a whole 200
    Seasonal cycle 200
      February 200
      April 202
      May 203
      June 206
      July 209
      Autumn 210
    Annual differences 212
  Vertical distribution 214
    Diurnal stratification 214
    Vertical stratification other than diurnal 217
  Comparison with other areas 221
Relative abundance of different species 228
    Monthly succession 230
      February 230
      April 231
      May 233
      June 237
      July 241
      Autumn 243
    Annual differences 245
  Sources of the local plankton 246
The area as a feeding ground for plankton-eating fish 253

Page

Conclusions 261
  The plankton as a whole 261
    Horizontal distribution 261
    Vertical distribution 264
    Annual differences 265
  Comparison with other areas 265
  Relative importance of different species 265
  Feeding conditions for plankton-eating fishes 268
Part II. Volumetric distribution of individual species 270
  Chordates 270
    Doliolum sp. 270
    Salps 272
    Fritillaria sp. 273
    Oikopleura dioica 273
    Oikopleura labradoriensis 274
  Molluscs 275
    Clione limacina 275
      Frequency 275
      Abundance 277
      Source of the local stock 278
    Limacina retroversa 279
      Frequency 279
      Abundance 280
      Vertical distribution 284
      Relation to temperature 284
      Annual variations 284
      Source of the local stock 284
    Other molluscs 286
  Decapods 286
    Crab and hermit crab larvae 286
    Crago sp. 289
    Palinurid larvae 290
    Lucifer typus 290
  Stomatopods 290
  Euphausiids 291
    Meganyctiphanes norvegica 291

Page
Nematoscelis megalops . . . 293
Thysanoessa inermis . . . 294
Thysanoessa gregaria . . . 295
Thysanoessa longicaudata . . . 296
Euphausiid larvae . . . 297
Other euphausiids . . . 298
Mysids . . . 298
Amphipods . . . 299
Euthemisto compressa . . . 299
Frequency . . . 299
Abundance . . . 300
Annual variations . . . 302
Other amphipods . . . 302
Copepods . . . 303
Acartia . . . 303
Anomalocera pattersoni . . . 304
Calanus finmarchicus . . . 304
Frequency . . . 304
Abundance . . . 305
Breeding periods . . . 310
Vertical distribution . . . 310
Diurnal migration . . . 312
Distribution in relation to temperature . . . 314
Annual fluctuations . . . 316
Calanus hyperboreus . . . 317
Candacia armata . . . 318
Centropages hamatus . . . 320
Centropages typicus . . . 321
Frequency . . . 321
Abundance . . . 321
Annual variations . . . 324
Vertical distribution . . . 324
Centropages violaceus . . . 326
Corycaeus sp. . . . 326
Eucalanus sp. . . . 326
Euchirella rostrata . . . 328

Page
- *Mecynocera clausi* 328
- *Metridia lucens* 329
  - Frequency 329
  - Abundance 331
  - Annual variations 333
- Oithona sp. 333
- Oncaea sp. 334
- Pleuromamma sp. 334
- *Paracalanus parvus* 336
- *Paraeuchaeta norvegica* 337
- *Pseudocalanus minutus* 338
  - Frequency 338
  - Abundance 339
  - Annual variations 340
- *Rhincalanus nasutus* 340
  - Frequency 340
  - Abundance 342
- *Scolecithrix danae* 343
- *Temora longicornis* 343
- *Temora stylifera* 345
- Other copepods 345

Cladocerans 346
- Podon and Evadne 346
- Penilia 346

Chaetognaths 347
- *Eukrohnia hamata* 347
- *Sagitta elegans* 347
  - Frequency 347
  - Abundance 349
  - Annual differences 351
  - Sources of the local stock 351
  - Vertical distribution 352
- *Sagitta enflata* 356
- *Sagitta serratodentata* 356
  - Frequency 356
  - Abundance 358

Page

        Annual variations 360
    Other chaetognaths 360
Annelids 361
    Tomopteris sp. 361
    Other annelids 361
Medusae 362
    Aglantha digitale 362
        Regional distribution 362
        Seasonal and annual variations 363
    Leptomedusae 365
    Other medusae 366
Siphonophores 366
    Agalmidae 366
    Muggiaea kochii 367
    Other siphonophores 367
Ctenophores 368
    Beroe sp. 368
    Pleurobrachia pileus 369
    Other ctenophores 370
Protozoans 371
Bibliography 372

INTRODUCTION

In April, 1929, the U. S. Bureau of Fisheries commenced an investigation of the distribution of the eggs and larvae of the mackerel in the waters of the continental shelf between Cape Cod and Latitude about 36°, a work continued during the vernal half year, in the three subsequent years. And while the collection of plankton was only a secondary goal, samples were systematically obtained on all cruises, and turned over to us for study.

Plankton investigations, we conceive, fall into two chief groups: (a) population and distribution studies of particular species or groups of species, or studies of the relationship of one species to another (e.g., feeding habits of fishes); and (b) attempts to assay the richness of one part of the sea or another, either in organic production, or as a feeding ground for larger animals. Studies of the first of these categories depend on enumerations of the specimens present, whether of different species or of different growth stages of given species. And the data that have been presented in the great majority of recent publications on zooplankton have been of this sort. If, however, we attempt to approach the matter from the other angle, information as to the mass of organic matter that is present in the sea from time to time and from place to place becomes of prime import. And very seldom can this be deduced from a knowledge of the numbers of units of which this mass is composed, because different planktonic animals, whether different species or different stages in the growth of one species, vary so widely in size that counts of total numbers are apt to prove very deceptive, if interpreted as indices to total mass. Part I of this report attempts to give at least a rough picture of the latter for the part of the sea in question, together with the proportions in which the leading species enter into it. Part II includes such information as to the distribution of individual species as our own analyses have yielded.

In studies of this sort, the vegetable and animal fractions of the plankton can be considered either as a unit, or separately: the latter course has seemed to us preferable, because of the basic difference between the nutritional requirements of the two categories. We must realize, however, whether for the zooplankton or for the phytoplankton, that measurements of mass—however precise these may be—are only one step in our path toward a knowledge of the productivity of the sea in organic substance. A second, coincident, and equally vital requirement is a knowledge of the rate of overturn, which can come only from population studies based on enumerations of individuals combined with classification of age-frequencies. A third essential step is the chemical analysis of the groups of organisms concerned, for these differ one from another, in the proportional components of proteins, carbohydrates, fats, and sundry other compounds.

The present report, confined to a survey of the mass distribution of the larger animal plankton, is offered in the hope that it may serve as a preliminary approach to the broader field outlined above.

The detailed data (which cannot be reproduced here for lack of space) are on file at the Woods Hole Oceanographic Institution.

ACKNOWLEDGMENTS

Mr. O. E. Sette, Dr. Roderick Macdonald, and Dr. George L. Clarke collaborated in identifying the plankton caught during 1929, Miss Alice Beale in identifying that caught during 1930 and part of 1931. And Dr. Th. von Brand has assisted us by making the ether extracts and the weighings used in our discussions of the area as a feeding ground for plankton-feeding fish.

GEOGRAPHIC LIMITS AND SUBDIVISIONS OF THE AREA

The account is confined to the continental shelf, out to the 200-meter contour, from the offing of Martha's Vineyard, westward and southward to about Latitude 36°. One cruise only (February 1931) extended south of Cape Hatteras. Neither was the number of hauls seaward from the 200-meter contour large enough, for any general estimate of plankton volumes in the slope water.

For convenience in regional comparisons, we have arbitrarily divided the area into a northern sector north from (and including) the Atlantic City profile, a southern sector, south of the latter, an inshore belt extending 30 miles out from the coast, and an offshore belt, thence seaward to the 200-meter contour (Fig. 1).

HISTORY AND SOURCES OF INFORMATION

So far as we have been able to learn, the first published account of the zooplanktonic communities of the region in question was Rathbun's (1889) report on tow-net catches made in April-May 1887, in connection with the mackerel investigations of that year. During subsequent years, several notices appeared of the occurrences of individual planktonic groups for restricted localities, e.g., of the copepods of the New Jersey coast (Fowler, 1912), of medusae, ctenophores, copepods, and amphipods, etc., of the Woods Hole region (Fish, 1925; Hargitt, 1905; Holmes, 1905; Mayer, 1912; Wheeler, 1901; Wilson, 1932), of copepods

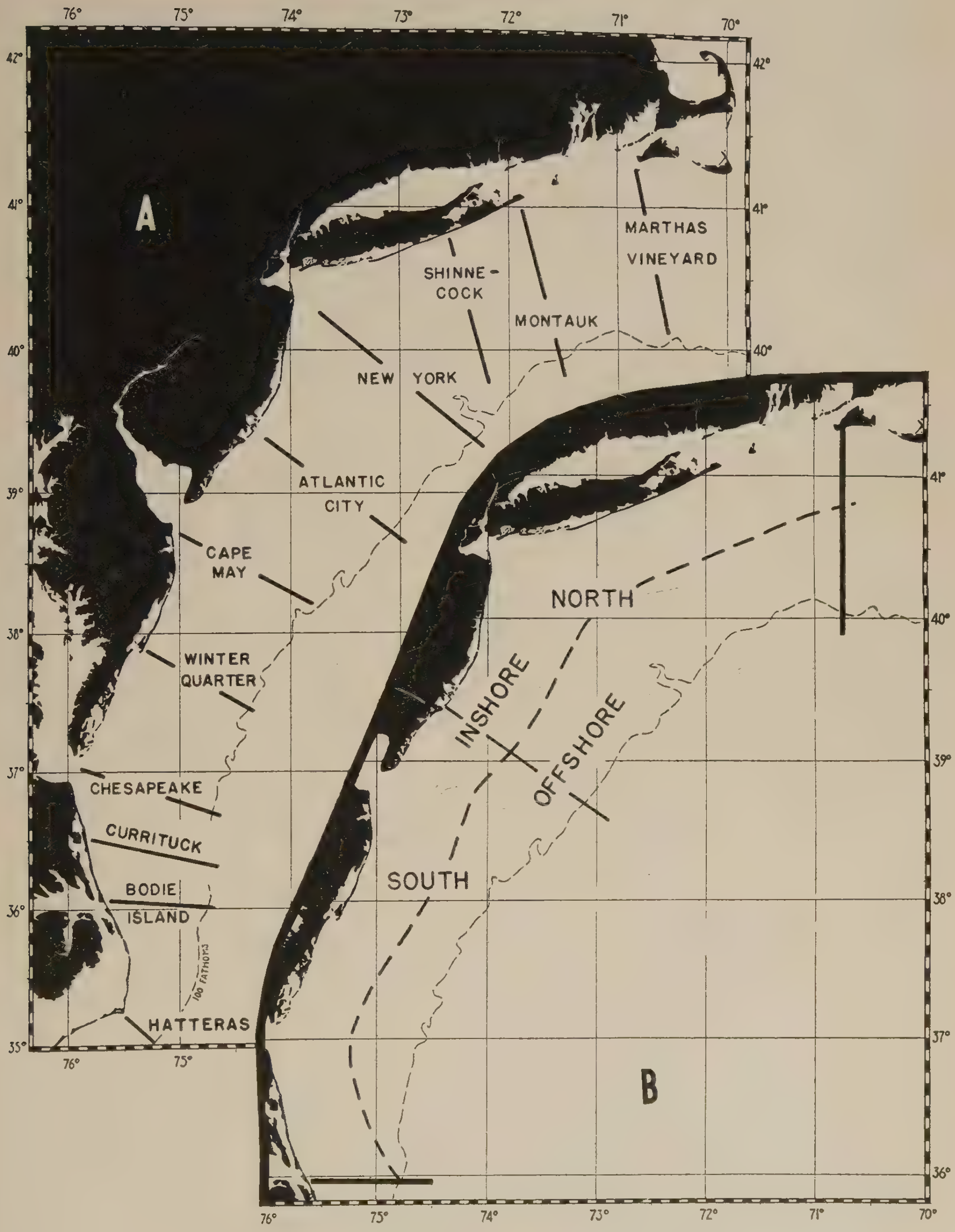

A
MARTHAS VINEYARD
SHINNECOCK
MONTAUK
NEW YORK
ATLANTIC CITY
CAPE MAY
WINTER QUARTER
CHESAPEAKE
CURRITUCK
BODIE ISLAND
100 FATHOMS
HATTERAS
B
NORTH
INSHORE
OFFSHORE
SOUTH
76°
75°
74°
73°
72°
71°
70°
42°
41°
40°
39°
38°
37°
36°
35°

Fig. 1. Charts of the area: A, Locations of profiles; B, Sub-divisions of the area as employed in the present report.

and other groups for Chesapeake Bay (Cowles, 1930; Wilson, 1932a). But it was not until 1913 that any systematic survey of the plankton of the continental shelf was undertaken. In that summer, the U. S. Fisheries Schooner "Grampus" collected samples at a grid of stations between the offings of Cape Cod and of Chesapeake Bay, as well as in the Gulf of Maine (Bigelow, 1915). And she surveyed these same waters again in 1916, both in August and in November (Bigelow, 1922). No data had, however, been obtained for any other year until 1929, when "Albatross II" carried out cruises in April, May, June, and July. And these were repeated in the following months and years:

1930—February, April (2 cruises), May, June (2 cruises), July;
1931—February, May, June, July;
1932—February, May (4 cruises), June (3 cruises).

"Atlantis" of the Woods Hole Oceanographic Institution, also made a cruise in October 1931. And periodic collecting was carried out from the Institution, both with a pump-filter and with tow nets, at a station a few miles off Martha's Vineyard, from late June 1935 to September 1936 (Clarke and Zinn, 1937).

We have drawn freely from all of the foregoing. But the collections made by the U. S. Bureau of Fisheries during the years 1929–1932, as outlined above have been the chief basis for the present report, which forms a sequel to earlier accounts of the temperature and of the salinity of the same region (Bigelow, 1933; Bigelow and Sears, 1935).

METHODS

Collection

The observing stations (with few exceptions) were located along the profiles indicated on Figure 1, so spaced that on each profile the inshore belt, the mid-belt, and the outer edge of the shelf were sampled at points seldom more than 15–20 miles apart, and often much closer (for position of stations, etc., see Bigelow, 1933, p. 104). The plan was for observations to be made at approximately the same localities, on all the cruises, and this was adhered to as far as practicable,[1] six hundred and four plankton stations on the continental shelf being occupied in all, 377 of them in the northern sector, 227 in the southern, 330 in the inshore belt, and 274 offshore.

Most of the hauls made by "Atlantis" in October 1931 were vertical, those by "Albatross II", in 1929, horizontal, at the surface, and (except when in very

[1] Bad weather sometimes interfered, and some of the cruises were abbreviated.

shallow water, or when the sea was very rough) at one or more subsurface levels at each station. In subsequent years, on "Albatross II", oblique hauls were employed to obviate the chief shortcoming of horizontal towing, namely, that it may be a matter of chance whether the net hits or misses the strata where the planktonic population is richest or poorest.[1]

Ideally, hauls of this type should be made by lowering the net close to the bottom and by towing in a diagonal direction up to the surface. This, however, is seldom practical, the best substitute being to tow in a series of short horizontal steps at frequent intervals from bottom to surface.

The standard procedure in the present case (seldom, however, attained *in toto*), was to tow for two minutes at each five meter level, the hauls often being abbreviated to one meter of towing at every ten meter level, at the deep stations, in order to shorten the time required. The column strained in this way diverged, on the average, by about 15° from the horizontal. At a towing speed averaging 1.2 knots or 37 meters per minute (as observed repeatedly), the oblique column fished through was thus about 370–518 meters long, at stations where the vertical depth was 20–30 meters, or about 777 meters where the depth was 200 meters. The chief drawback to hauls of this sort, from near bottom to surface, is that they give no information as to the degree of stratification of the communities at different levels. To meet this difficulty, two or more nets were attached on the wire at a time, 20–35 meters apart, on the cruises subsequent to February 1931. Unfortunately, a considerable proportion of the hauls left, unsampled, a stratum next the bottom, equalling as much as 50% of the whole vertical distance in extreme cases.

The nets were either 1-meter, or ½-meter in diameter, of silk, the forepart with 29–38 meshes per linear inch, the rear part with 48–54 meshes per inch. Nets of these meshes and diameters may be expected adequately to sample planktonic animals of the various groups from the size of the copepod, Centropages, up to fish fry. Many or most of the smaller adult copepods (Oithona), smaller larval copepods of all species, and other minute animals pass through. And failure to sample these is mentioned repeatedly in the following pages.

MEASUREMENTS AND CALCULATIONS

Dry weight would be the most reliable index, easily obtainable, to the mass of the plankton, if the desiccation and weighing could be done soon after the collections were made. But, for so large a number of samples, this would have required much more assistance than was available. And so much of the oil from copepods—and other substances as well, both from these and from other groups—dissolves out into the preservative that long preservation of the samples robs dry weighing of much of its initial advantage over volumetric measurement, which is a much simpler procedure.

---

[1] For a recent discussion of the advantages of oblique towing, see Walford, 1938.

We may also point out that "volume" is usually translatable into "wet (preserved) weight" within a reasonable limit of error, for while the specific gravities of different groups of planktonic animals differ considerably—both in life and after preservation (e.g., as between shelled pteropods and ctenophores), this is comparatively constant within each of the major groups.

Selected samples, from the collections of 1929, showed the following weight-volume relationship, when weighed in water:

Calanus, 20 c.c. by displacement; "wet weight," 18.35 gms;
Sagitta elegans, 20 c.c. by displacement; "wet weight," 21.34 gms;
Limacina, 20 c.c. by displacement, "wet weight," 20.18 gms.

The method of volumetric measurement that has most often been used in the past consists simply of allowing the catch to settle for a given length of time, in a graduated cylinder of convenient size, and of then measuring its bulk. It has, however, been universally appreciated that the resultant measurements have only a comparative value, because they include the interspaces between the animals, as well as the latter themselves. Savage (1931, p. 5) has, in fact, shown that such measurements may average more than twice as large as those obtained, for the same samples by the so-called displacement method.[1] And comparative tests, that we have made for the entire series of "Albatross II" catches for the year 1929, have similarly shown a wide disparity, with volumes averaging 2–4 times as large by "settlement" as by "displacement," for all types of plankton combined, the difference being greatest for plankton dominated by sagittae (extreme case, 105 c.c. by displacement; 935 c.c. by settlement), least for plankton consisting chiefly of Calanus (210 c.c. by displacement; 260 c.c. by settlement). All measurements in the present report have, therefore, been made by displacement as follows:

The sample of plankton is first drained, through a bolting silk strainer with meshes as fine as that of the nets in which the catch was taken. The semi-dried mass is then added to a known volume of water, when the resultant increase in volume is equal to that of the sample, plus the few drops of liquid that may still adhere to the latter after draining.

---

[1] See Johnstone, 1908, p. 130 for a general discussion of these methods.

In the preliminary catches of 1929, the respective percentages of the several constituent species or groups were determined either after these had been sorted out, or in some cases, roughly estimated. In the subsequent catches, the volumes of the species represented were arrived at as follows:

The total catch was first sorted into such of its constituent parts as were most readily separable, e.g., into the chaetognaths, euphausiids, larger medusae, adult amphipods, pteropods, and "residue," this last consisting chiefly of copepods, with other forms of similarly small size. Each of these groupings was then measured by the same displacement method as used in obtaining the total volume. A random and well mixed sample of at least 100 specimens[1] was then taken from each grouping, and the number of specimens counted, for each species represented. In order next to calculate the proportional volumes of the several species included in each grouping, and so to arrive at the total volume of each species in the total catch, it was necessary to weight each according to the average size of its members. In the cases of *Calanus finmarchicus*, *Centropages typicus*, and *Thysanoessa inermis*, the weightings were based on actual measurements of the volume per 100 specimens of large series of adults, covering the average size range. Volumetric comparison with these, by eye, then gave a rough ratio for weighting the younger stages of these same species, as well as for the other species.

The following actual example may serve more graphically to illustrate the procedure:

Station, Montauk V, June 12, 1930, total volume of catch, 60 c.c., or 480 c.c. per 20 minutes towing with a 1-meter net; volume of "residue," 59 c.c., or 472 c.c., per standard tow; number of individuals of each species represented among 119 counted specimens in sample of "residue", 61 *Calanus finmarchicus*, 1 *Centropages typicus*, 52 *Metridia lucens*, 5 *Pseudocalanus minutus*. Weights derived as above, Calanus, 25; Centropages, 4; Metridia, 25; Pseudocalanus, 2. Calculated percentages (volumetric), in "residue", Calanus, 53.7%; Centropages, 0.1%; Metridia, 45.7%; Pseudocalanus, 0.3%. The volume of "residue" being 472 c.c. for the standard haul, the calculated volumes for the several species work out at 253 c.c. of Calanus; < 1 c.c. of Centropages; 216 c.c. of Metridia, and 1 c.c. of Pseudocalanus.

Comparison of catches made in horizontal hauls at the surface and deeper in 1929, and in oblique hauls through shoaler and deeper sections of the water column in 1931 and 1932, afford some information as to the degree of stratification of the plankton in different months. Since open nets were used, it is obvious that the volumes taken in the deeper tows represent not only the abundance prevailing at the towing level, but also whatever was caught while the nets were being lowered and hauled in again. And this contamination might well be great enough entirely to obscure the picture in individual cases—if, for example, it chanced that the net was hauled up through a dense swarm of one organism or another. But at most of the stations, inside the 200-meter contour, the vertical sectors averaged less than 1/7 as long as the horizontal sectors in the cases of the horizontal hauls, and only about 1/15 as long as the horizontal sectors in the cases of obliques. It may, therefore, be assumed that this contamination is not an important factor for our purposes in these shoal waters, when considerable numbers of catches are averaged. Consequently, we have not attempted to correct for it.[1]

---

[1] Fewer, if there were not that many.

In order to render the catches made in horizontal tows comparable (from the standpoint of depth) with those made in obliques, we have further assumed that the catches of the latter may be accepted as representative of the mid-depths of the water columns sampled. And the depths stated in the following discussion are so derived.

We have credited a value of 1 to catches < 1 c.c., in the calculations of average volumes and ratios, while in the case of the latter, we have also treated values of 0 as equivalent to 1 c.c., for the sake of simplicity. Likewise, in the tables giving percentages and abundance, a dash signifies that the particular subdivision was not visited on a particular cruise; a 0 that the species was not detected in that particular subdivision, though taken in another; a blank that it was not detected in any subdivision on a particular cruise.

Expression of Results

The fact that the catches were taken in nets of different sizes, as well as in hauls of different lengths, some oblique, some vertical, and some horizontal, makes it necessary to reduce all the measurements to one common basis in order to render the results comparable, one with another.

The elements on which such a reduction must be based for any particular haul are:— (a) the diameter of the net used, (b) the duration of the haul in time, (c) the average speed of the vessel (or else the linear extent of the haul), and (d) the efficiency of the particular net used. In the cases of horizontal and oblique hauls, the first two elements are precisely known, hence the first reduction is to "catch per unit time per unit net-opening"; the standards here adopted being 20 minutes of hauling with a net 1 meter in diameter. Up to this point, the reduction is precise mathematically. But it does not yet provide a standard of comparison, unless "time" can be translated directly into "length of water column fished". Close attention was, therefore, paid to the speed of the ship, on all the cruises of "Albatross II" and of "Atlantis", and records by R.P.M. of the propeller, and by ship's log, show that this was close to 1.2 knots for the series as a whole. But whoever has had experience with the differences in the velocities and directions of currents at different levels in coastwise waters where the circulation is governed by the tide, will appreciate that the rate at which a ship is moving, relative to the surface water may differ considerably from the rate of a net relative to the water at some deeper level. Rather than attempt the calculation of the linear extent of each individual tow, we have, therefore, thought it preferable to assume an average speed of 1.2 knots in all the calculations, and the catches of the horizontal and oblique hauls were reduced to the common standard accordingly.

---

[1] For a case of such correction, see Bigelow and Sears, 1937, p. 69.

On this basis, the linear extent of the standard tow of 20 minutes would average 741 meters. And there would be as good justification for expressing the volumes caught "per unit volume of water" as "per unit time," for the one of these expressions includes the same probable errors as the other. But we must impress upon the reader that neither of these expressions is susceptible of direct translation into "volume of plankton present," whether per unit time or per unit volume of water, because of uncertainty as to the efficiency of the nets (discussed on p. 198). Hence, to avoid any possible misconception as to the reliability of the observations, we have endeavored to draw a sharp distinction, in this respect throughout the descriptive sections of the present report. It has also been suggested to us that "catch per unit volume of water" might suggest a higher degree of precision than "catch per unit tow", whereas actually the two are interchangeable. We have, therefore, adopted the latter.

All the results, then, are expressed as catch, in c.c. per 20 minutes towing with a 1-meter net at an assumed speed of 1.2 knots (2222 meters per hour), unless otherwise stated.

VALIDITY OF CALCULATED RESULTS

No modern student of plankton, we fancy, would claim that quantitative calculations, based on tow nettings, can be any more than approximations to the truth.

To begin with, we must face what may be termed the "catching error" inherent in the tow net method. We have no intention of reviving the controversies as to the reliability of the latter that gave planktonologists so much concern during the last quarter of the nineteenth century. It seems pertinent, however, to remind the reader that a tow net, of the usual conical form, and of mesh appropriate for the capture of planktonic organisms, filters somewhat less than the amount of water that would pass through a simple hoop of equal diameter, the loss (i.e., the amount regurgitated) depending on the shape of the net, on the proportionate areas occupied by the threads and by the spaces between the latter, and on the pressure, i.e., on the velocity with which the net is drawn through the water. The slower the towing, the more complete filtration, as every planktonologist knows from observation. In the case of fine meshed silk (e.g., #20), the loss may be so serious at ordinary towing speeds as to necessitate special types of net, to increase the filtering surface relative to the mouth opening. And even with silk as coarse meshed as #0 (38 meshes per linear inch), such as used in the fore parts of our nets, only about 30% as much water would pass through a given area, drawn transversely at 2 knots, as through an open cylinder of the same area, according to the relationship between pressure and filtration in Hensen's (1895) experiments[1].

This loss is so minimized by the increase in straining area relative to mouth opening, resulting from the conical form, that it probably averaged less than 10%, at the usual towing speed for our nets, though experiments at various hands have proved that the catches made in parallel hauls with similar nets may vary as much as 10–30% or even more (see Winsor and Walford, 1936, p. 190, for a recent discussion). Neither is clogging likely to be serious, for nets such as those used, except on rare occasions when diatoms or Phaeocystis may swarm, or when the gelatinous bodies of ctenophores, appendicularians, etc., may block the meshes. Much more serious is the uncertainty as to what relation the fraction of the plankton that is adequately sampled bears to the remainder that the net fails to capture, it being common knowledge that no one type of net will equally well sample the various size categories of planktonic animals. The nets used in the present studies (meshes, 38–54 per linear inch) being comparatively coarse, the failure of small copepods such as Oithona, or the young of others, to figure more largely in the following volumetric lists, does not necessarily mean that they may not actually have been present in considerably greater abundance (numerically, at least) than the catches would suggest.

---

[1] Pressure at the given velocity calculated from the formula, $p=\sqrt{\frac{v^2}{2g}}$.

In extended surveys, errors also creep in through the fact that it is necessary to classify the hauls by the time—i.e., by the duration of the tow—, for in most cases, no precise measure of the speed of the net through the water, i.e., the distance, is available, as already remarked (p. 196).

While errors of the sorts just mentioned may reach extreme proportions in individual cases, they can usually be minimized by combining a sufficiently extensive series of data. More vital is the question whether the grid formed by the stations, in any particular plankton survey, has been close enough to warrant generalization for the included area as a whole. In this respect, the consistency of results seems to us sufficient warrant, as already argued by Walford (1938) for a similar survey carried out on George's Bank.

If these shortcomings of various kinds should chance to be cumulative for a given haul, the calculated volume for the latter may very likely be as much as 100% in error—perhaps more. But, when so many observations are in hand, the plus or minus error no doubt averages much less than this—perhaps not more than 20–30%, which is far smaller than the variations observed among the values that form the basis of study. And since the latter also show very clear consistency, both regional and secular, not only for the volumes of plankton as a whole, but also for the more abundant of the constituent species, we think no further argument is needed in justification of our conclusion that the picture they have yielded may be accepted as representative (within reasonable limits) of the larger zooplankton from place to place within the area, from season to season, and from year to year, for the period 1930–1932.

The basis for comparison between this group of years and the year 1929 is not so solid, because of the use in that year of horizontal hauls. The best we can do, in this case, is to assume that the average catch, of the two or more of these that were made at different levels at each station, at least approximates the correct average for the water column as a whole, bottom to surface. It is probable that this is close to the truth through the period February-April, i.e., before any marked stratification has developed. But from June on, as the plankton like the temperature tends to become increasingly stratified, it becomes increasingly doubtful how thick the stratum is, for which the yield of a net working horizontally, at any particular level, can be accepted as representative.

PART I. THE VOLUME OF THE ZOOPLANKTON AS A UNIT

The Water Column as a Whole

The volumes in c.c. per standard haul for each month of the series are shown on Figures 2–6, 8–9, and average and maximum volumes for the several subdivisions in the following table:

Month	Year	Inshore		Offshore		North		South		Total area Surveyed	
		Av.	Max.	Av.	Max.	Av.	Max.	Av.	Max.	Av.	Max.
February	1930	249	1000	49	128	111	497	175	1000	144	1000
	1931	218	432	109	140	57	108	200	432	153	432
	1932	550	2400	83	306	57	91	472	2400	368	2400
April	1929	203	520	349	1701	312	520	224	1701	263	1701
	1930	302	1124	322	1026	396	1124	244	700	199	1124
May	1929	243	1448	326	805	334	805	198	1448	273	1448
	1930	467	1294	1026	3288	689	1847	746	3288	714	3288
	1931	385	821	622	1880	507	1880	436	821	487	1880
	1932	274	771	329	1026	285	1026	320	746	299	1026
June	1929	174	541	294	447	249	541	168	514	219	541
	1930	430	1712	311	789	420	1712	242	900	381	1712
	1931	535	978	777	1756	654	1756	578	1373	626	1756
	1932	232	478	302	790	228	467	333	790	261	790
July	1929	296	550	211	474	285	550	203	512	257	550[1]
	1930	600	1681	341	800	448	1681	—	—	448	1681
	1931	702	1410	912	2341	782	2341	—	—	782	2341
October	1931	—	—	234	560	236	331	231	560	234	560

[1] One haul of 67109 c.c. omitted.

The most striking feature of volumetric distribution throughout has been the irregularity from station to station, often with volumes differing up to a hundred fold, between localities only a few miles apart. As a concrete illustration, we may instance the fact that the maximum volume was 3 times as large as the minimum, even on the cruise (May 24–28, 1932) when the difference between the two was smallest. And on the occasion, when widest (July 10–18, 1930), the range was 373 to one.

Comparatively regular gradients nevertheless appear, both secular and regional, when averages are compared, for subdivisions large enough to include several stations each, as follows:

Seasonal Cycle

February. February may be chosen as the starting point in our survey, it being highly probable (though not yet actually proven) that the zooplanktonic community in the waters in question, as in boreal seas in general, is at its lowest ebb, at the end of winter, or in early spring.

The three surveys for this month (1930, 1931, 1932) agree in showing the volumes as largest over the inner half of the shelf, and to the south, decreasing offshore and to the north (Fig. 2), though with great irregularity from station to station, as is, in fact, the case throughout the year.

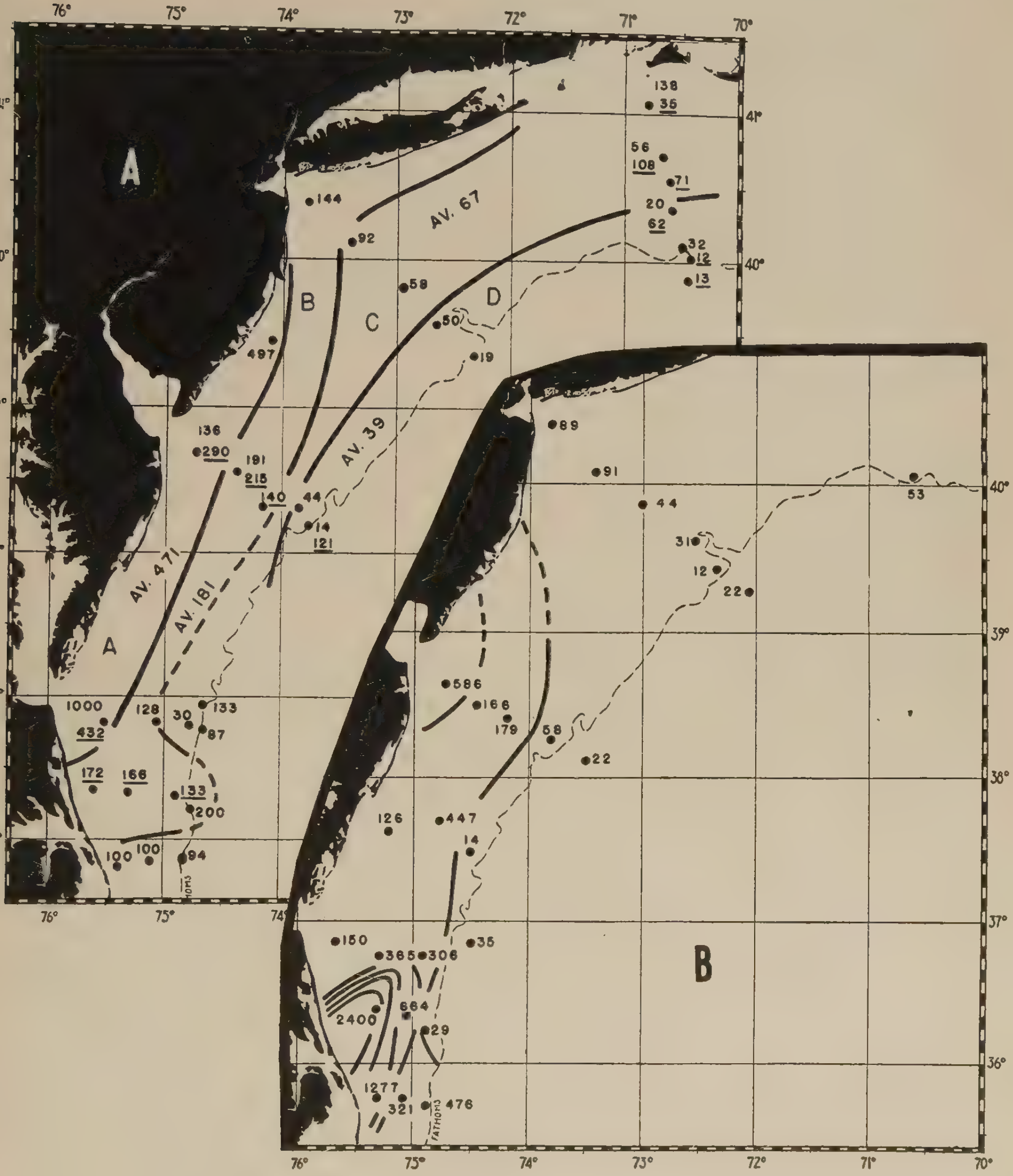

76°
75°
74°
73°
72°
71°
70°
41°
40°
39°
38°
37°
36°
A
B
C
D
AV. 67
AV. 39
AV. 471
AV. 181
138
35
56
108
71
20
62
32
12
13
144
92
58
50
19
497
136
290
191
215
140
44
14
121
1000
432
128
30
133
87
172
166
133
200
100
100
94
89
91
44
53
31
12
22
586
166
179
58
22
126
447
14
150
365
306
35
2400
664
29
1277
321
476
FATHOMS
B

Fig. 2. Volumes of plankton, per standard haul: A, February 5-13, 1930 and February 13-March 5, 1931 (underlined); B, February 10-March 1, 1932, contour lines 100, 500, 1000, 1500, 2000 c.c.

The magnitude of this inshore-offshore gradient in winters of normal temperature may be illustrated by the fact that, of the 37 tows made in 1930 and 1931, the average of the ten closest to shore was 294 c.c., four yielding more than 250 c.c., with fourteen hauls over the mid-belt of the shelf averaging 104 c.c., whereas thirteen along the continental edge averaged only 72 c.c., with four alone of the latter yielding as much as 100 c.c. The plankton thus averaged roughly twice as voluminous inshore as along the mid-belt of the shelf, four times as voluminous as along the outer edge of the latter. And in most cases the inshore-offshore relationship was of this same order along individual profiles, though with occasional exceptions as in 1930 off Cape May, where the volume was 136 c.c. at the inshore station, but 191 c.c. at the station next seaward, and again in 1931, off Martha's Vineyard where the catch closest to land was only 35 c.c., but 108 c.c. farther out.

The contrast prevailing at this season between small volumes in the northeastern sector (bounded by the New York profile) and large in the southern is even more striking, February volumes having averaged only about 1/3 as great for the former as for the latter in 1930 and in 1931 combined, and 1/10 as great in 1932. Furthermore, no catch as great as 200 c.c. was made in the eastern sector in any February, whereas fourteen such February catches were recorded to the south and west. But this abundance seems not to extend south of Cape Hatteras "which may be regarded as the southern boundary in winter to the cold boreal water" (Bigelow, 1933, p. 11), tows made in 1931 in the vicinity of the Cape having yielded only 15, 80, 92, and 205 c.c. respectively.

April. The sequence of events in the development of the plankton, with the advance of spring, is obscured in our data by the long period that elapsed between the first and second surveys of each year, no collections having been made in March. In 1930, which we must perforce accept as representative, being the only year when collections were made both in February and in April, average volumes had increased about eight or nine fold from the one month to the other over the offshore belt, northward and eastward from the Barnegat profile, where the catch averaged 325 c.c. in early April, contrasting with 39 c.c. in February. In the southern sector, however, the volume of plankton still averaged about the same order of magnitude in April (244 c.c.) as it had in February (175 c.c.).

This combination of relatively stationary conditions in the south, with marked augmentation in the north resulted—in the year in question—in a reversal of the north-south relationship that existed in February, so that by early April, the volume of plankton averaged nearly three times as great (419 c.c.)

eastward from the New York profile, as south of the latter (157 c.c.), instead of only about 1/3 as great, as it had at the end of the winter, this being a case where the north-south gradient would have been hidden, had the comparison been made between sectors separated by the boundary (Atlantic City profile) that has usually proved significant.

Unfortunately, it was not possible to include the immediate offing of Chesapeake Bay in this calculation, lacking an oblique haul there in that April. A very rich surface catch (1200 c.c.) was made there, it is true, in that month, but we have no information as to whether the average volume had or had not increased at this particular locality meantime. And volumes for April similarly averaged larger in the northern sector than in the southern in 1929, as well.

Vernal augmentation spread southward in 1930, between the first and third weeks of April as far as the offing of Chesapeake Bay, causing a five-fold increase since February, along the mid-belt of the shelf, as illustrated by the expanding outlines of the area where the catches were greater than 500 c.c. (Fig. 3A, B). And there is evidence of some slight alteration of the same order to the south of the Bay as well, where the late April average was 181 c.c. (6 stations, oblique hauls), contrasting with 98 c.c. (3 stations, 1 oblique, 2 horizontal hauls), early in the month. Consequently, the plankton averaged much the richest along the mid-belt of the shelf by mid-April of that year (16 stations, average, 496 c.c.),[1] whereas the coastal waters—which had been richest in February—were now relatively barren (8 stations, average, 192 c.c.), as was also the case along the continental edge (8 stations, average, 133 c.c.).

The facts, (a) that the richest aggregations recorded for February and April (Fig. 2, 3) have not been at the most easterly stations, and (b) that the plankton of the Gulf of Maine is on the whole sparse in late winter and early spring (Bigelow, 1926; Fish and Johnson, 1937), combined with the vernal histories of the dominant species, individually, is sufficient evidence that in years when volumes increase significantly in early spring, this results chiefly from local reproduction, not from immigration from waters farther to the east. Neither have we any evidence of mass immigration from offshore, or from the south, at this season.

May. In one of the years (1930) when April can be compared with May, the area that had been well populated (> 500 c.c.) during the earlier month, had expanded seaward to the continental edge, by the latter, all along from the offing of Chesapeake Bay to that of Montauk (though apparently no farther eastward),

---

[1] In early April, only two stations yielded more than 500 c.c. (Fig. 3A), both of them east of New York. In late April this was the case at nine stations scattered as far south as Chesapeake Bay.

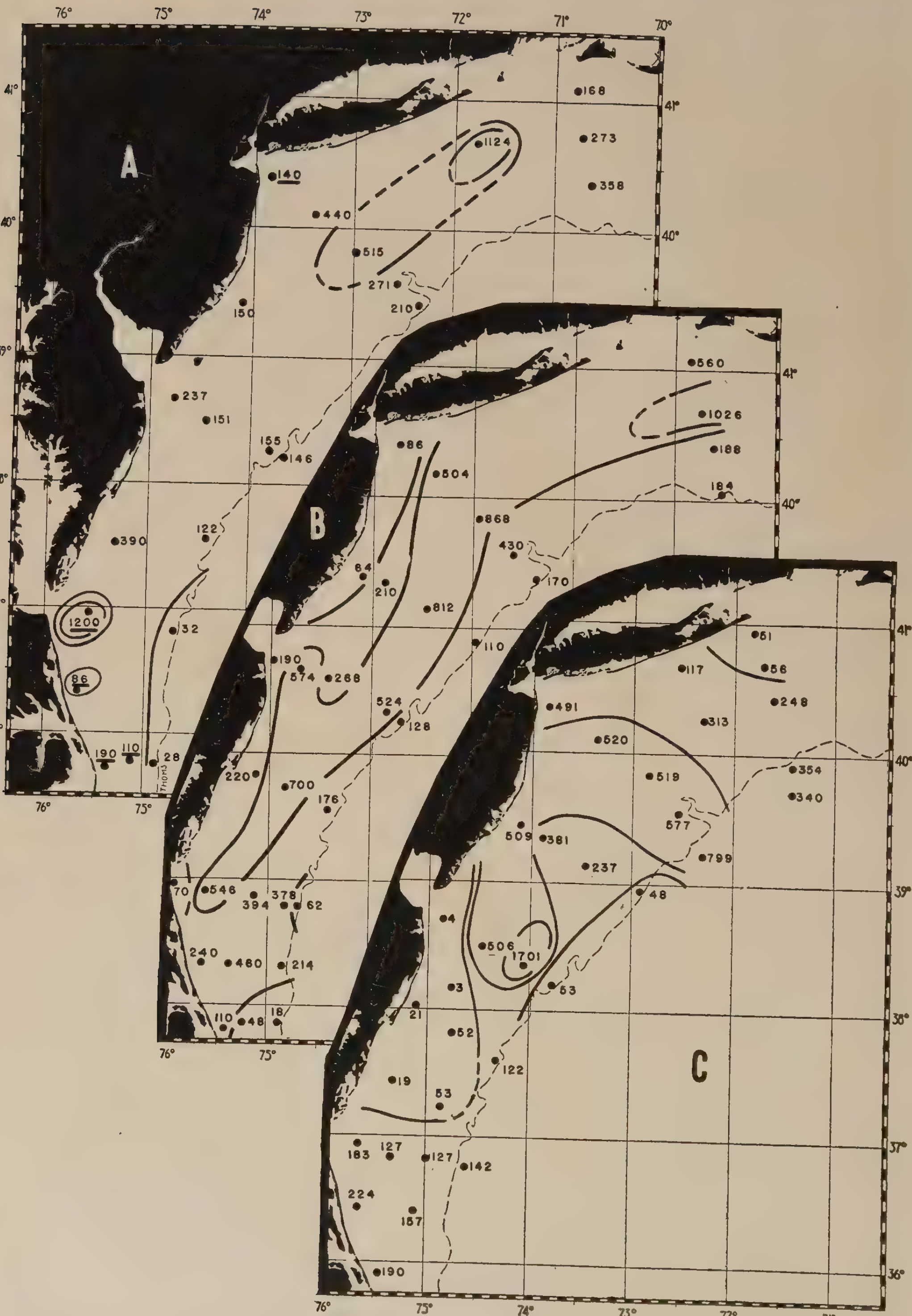

A
B
C
76°
75°
74°
73°
72°
71°
70°
41°
40°
39°
38°
37°
36°
168
273
358
1124
140
440
515
271
210
150
237
151
155
146
122
390
1200
86
132
190
110
28
560
1026
188
184
86
504
868
430
170
64
210
812
110
190
574
268
524
128
220
700
176
70
546
394
378
62
240
460
214
110
48
18
51
117
56
248
491
313
520
519
354
340
577
509
381
799
237
48
4
506
1701
3
53
21
52
122
19
53
183
127
127
142
224
157
190

Fig. 3. Volumes of plankton, per standard haul, contour lines for 100, 500, 1000 c.c: A, April 3-11, 1930, with surface hauls underlined: B, April 22–May 1, 1930; C, April 14–24, 1929.

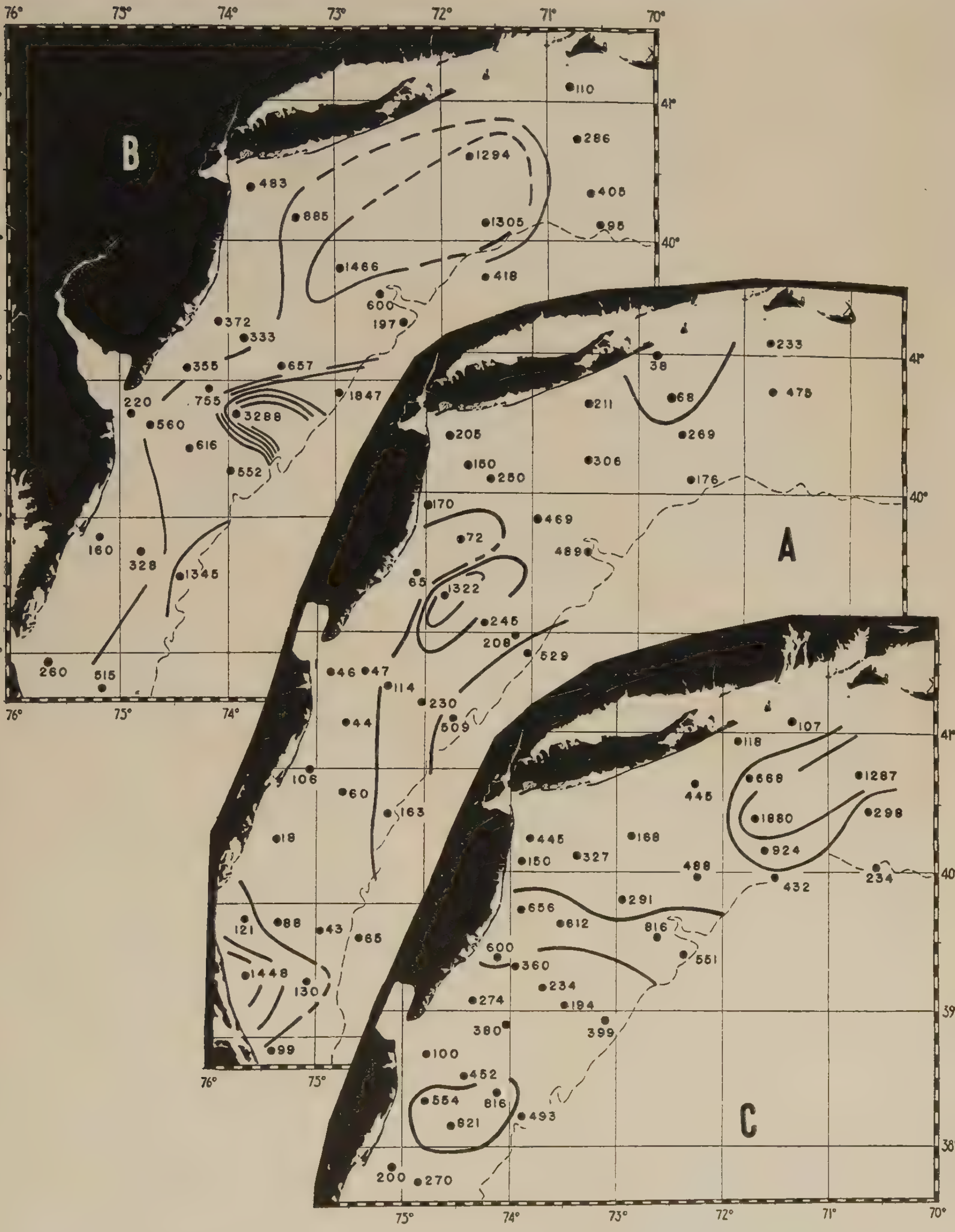

76°
75°
74°
73°
72°
71°
70°
41°
40°
39°
38°
37°
B
110
286
1294
405
483
885
1305
95
1466
418
600
197
372
333
355
657
220
755
1847
3288
560
616
552
160
328
1345
260
515
233
38
475
68
211
269
205
306
150
250
176
170
469
72
489
A
65
1322
245
208
529
46
47
114
230
44
509
106
60
163
18
121
88
43
65
1448
130
99
107
118
1287
668
445
1880
298
445
168
924
150
327
488
432
234
291
656
612
816
600
551
360
234
274
194
380
399
100
452
554
816
621
493
C
200
270

Fig. 4. Volumes of plankton, per standard haul, contour lines 100, 500, 1000, 1500, 2000, 2500, 3000: A, May 10–18, 1929; B, May 12-23, 1930; C, May 16–22, 1931.

coupled with the development of considerable pools richer than 1000 c.c. (Fig. 4B). A considerable increase in the volumes of plankton had also taken place inshore between the offings of Delaware Bay and of New York, where three stations now averaged 358 c.c., contrasting with only 113 c.c. at the end of April. As a result of these changes, the volume of plankton averaged approximately twice as great in that May as it had in April, both in the northern sector and in the southern, with an alteration of the same order, inshore as well as offshore. But it is doubtful whether any significant or general alteration had taken place in this respect from the one month to the next, in 1929. In fact, the volume of plankton may not have averaged significantly higher in April or in May of that year than at the end of the preceding winter.[1] And it is certain that no significant augmentation took place between February and May in 1932, contrasting with the great increase that certainly took place during that interval both in 1930 and 1931 (Fig. 4), unless possibly for a brief period in March or April, months for which no information is available for that particular year.

Averages for the different subdivisions suggest, however, that differences from year to year in these respects are not wide enough to obscure the general rule that in May the offshore belt supports an appreciably larger volume of plankton than the inshore belt (in fact, this was the case to a greater or less extent in each year). But no prevailing difference for this month is suggested, between the northern sector and the southern.

June. In one year of the series (1931) the average volume continued to increase somewhat in each subdivision, from May to June (Table, p. 200). In each of the other three years, a decrease was, however, recorded. Thus, in 1929, when the rich (>500 c.c.) areas continued about as scattered in June as in May (Fig. 4A, 6A), average volumes fell between mid-May and early June from about 334 c.c. to about 249 c.c. in the northern sector, from 198 c.c. to 168 c.c. in the southern with corresponding decreases in the maxima from 1448 c.c. in May to 541 c.c. in June. And it appears that the vernal maximum,—whether for extent of the rich (>500 c.c.) area, or for average and maximum volumes,—was also reached by May, in 1930, for in that year the average volume for the area as a whole[2] decreased from about 714 c.c. in that month to about 381 c.c. for June, the rich (> 500 c.c.) areas meantime contracting by the end of the latter month to a few scattered centers, one close to Delaware Bay (due to a local swarm of *Sagitta*

---

[1] We have no February data for 1929.

[2] The June cruises of 1930 extended southward only as far as the mouth of Delaware Bay.

elegans), one near the edge of the shelf off New York, and others near shore off Montauk Point and Martha's Vineyard (Cf. Fig. 4B with Fig. 5B). And seven successive surveys (Fig. 7), at close intervals in 1932, again showed the trend as

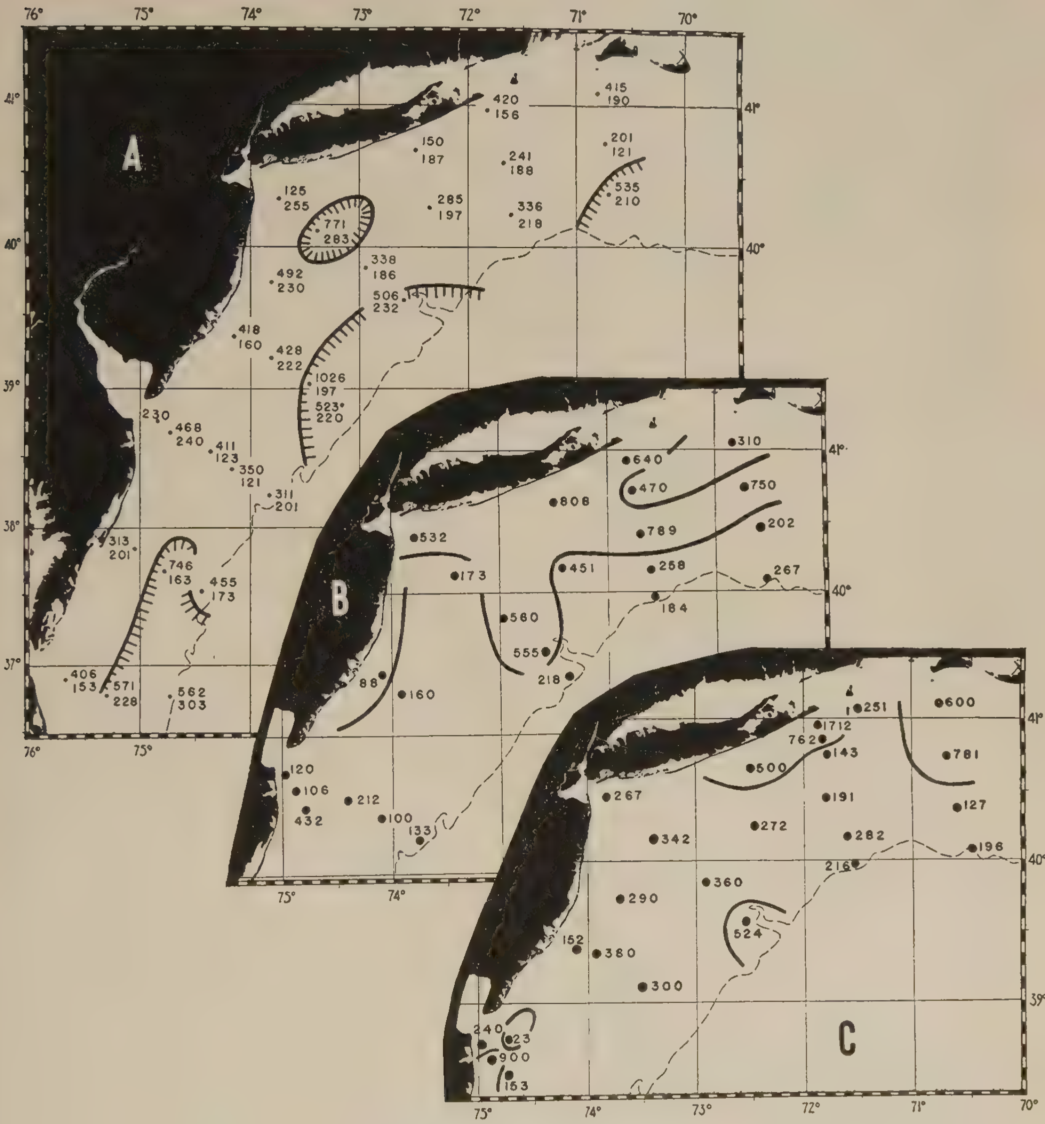

76°
75°
74°
73°
72°
71°
70°
41°
40°
39°
38°
37°
A
415 190
420 156
150 187
241 188
201 121
535 210
125 255
285 197
336 218
771 283
338 186
492 230
506 232
418 160
428 222
1026 197
523 220
230
468 240
411 123
350 121
311 201
313 201
746 163
455 173
406 153
571 228
562 303
B
310
640
470
750
808
789
202
532
173
451
258
267
184
560
555
218
88
160
120
106
432
212
100
133
C
251
600
1712
762
143
781
500
267
191
127
272
282
342
196
216
360
290
524
152
380
300
240
23
900
153

Fig. 5. Volumes of plankton, per standard haul: A, maximum and minimum at each station for the four May cruises of 1932, hatched areas where catches were greater than 500 c.c.; B, June 7–18, 1930; C, June 24–July 1, 1930. Contour lines 100 and 500 c.c. in B and C.

generally downward from early May (299 c.c.) to late June (261 c.c.), except in the southernmost sector, an alteration which seems sufficiently consistent to be accepted as significant, though not large.

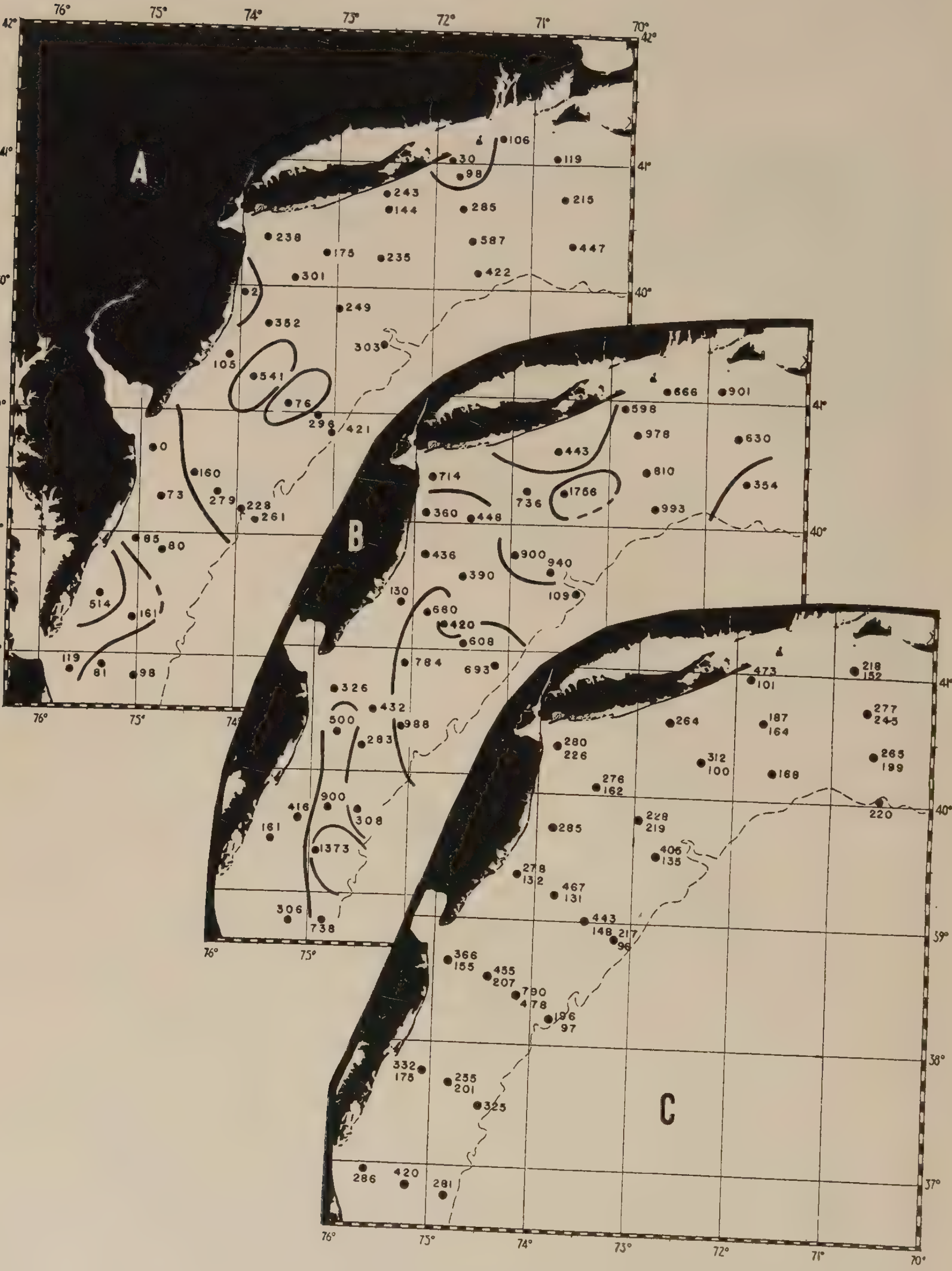

A
76°
75°
74°
73°
72°
71°
70°
42°
41°
40°
39°
38°
37°
106
30
119
98
243
144
285
215
238
175
235
587
447
301
422
2
249
352
303
105
541
76
296
421
0
160
73
279
228
261
85
80
514
161
119
81
98
B
666
901
598
978
630
443
810
714
1756
354
736
360
448
993
436
900
940
390
109
130
680
420
608
784
693
326
432
500
988
283
900
416
308
161
1373
306
738
C
473
101
218
152
264
187
164
277
245
280
226
312
100
168
265
199
276
162
228
219
220
285
406
135
278
132
467
131
443
148
217
96
366
155
455
207
790
478
196
97
332
175
255
201
325
286
420
281

Fig. 6. Volumes of plankton, per standard haul, contour lines 100, 500, 1000 c.c: A, May 28–June 5, 1929; B, June 12–19, 1931; C, maximum and minimum at each station for the three June cruises of 1932.

Thus, it appears that while the alteration—for the area as a whole—is not likely to be great in either direction, from May through June, the trend is more likely to be downward than upward, at this season in any given year.

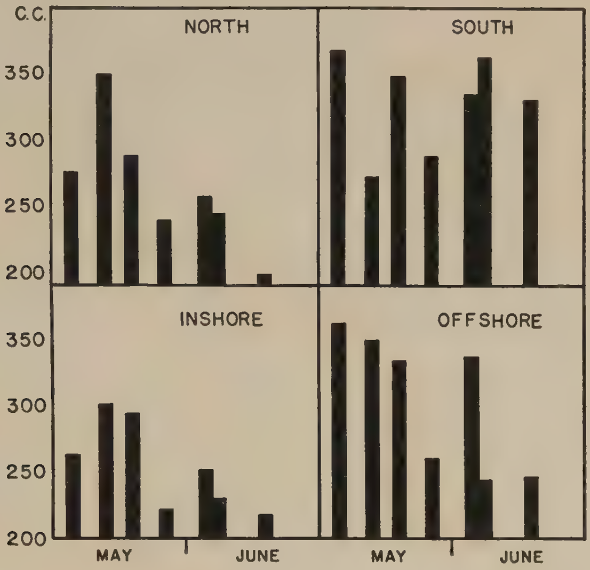


Fig. 7. Average volumes of plankton, in the different subdivisions, in May and June, 1932.

July. In the only year (1929), when a general survey was carried out in July, as well as in June, the average volume of plankton had ostensibly increased somewhat from the one month (June, average, 219 c.c.) to the next (July, average, 257 c.c.),[1] southward from the New York profile, but had decreased somewhat near the eastern boundary of the area (average, Montauk-Martha's Vineyard profiles, 275 c.c., in June; 250 c.c. in July). And while these changes were so small that they may best be interpreted as evidence of a roughly stationary state, so far as the average abundance is concerned, a corresponding shift in the center of population from east of the New York profile to south of the latter, may be regularly characteristic of this season, since a similar shift, westward, also took place between mid- and late June and mid-July of 1930 and 1931, as illustrated by the following average volumes for the Martha's Vineyard and Montauk profiles, contrasted with the New York and Barnegat profiles:

Year	Season	Barnegat-New York	Martha's Vineyard-Montauk
1930	Late June	327	478
	Mid-July	605	403
1931	Mid-June	535	730
	Mid-July	852	711

---

[1] One large haul (67109 c.c.) omitted from calculations of the July value.

An interesting feature of the volumetric picture for July is the striking irregularity of distribution, with centers of great abundance sporadically scattered on the shelf. In such cases, it is not unusual to make a poor catch close to an extraordinarily rich one. One haul, for example, off Montauk, on July 10, 1930, produced only 3 c.c., but another not ten miles away yielded 1120 c.c., chiefly, *Calanus finmarchicus*. And other instances of this same sort might be cited, On the other hand, three productive (> 500 c.c.) hauls from contiguous localities (Fig. 8A) in the offing of New York may perhaps have formed part of a center of abundance to the south of the area surveyed in that July.

Autumn. No quantitative information is available for the months of August and September. In 1931 (Fig. 9B), however, the volume of plankton in the offshore belt had decreased from an average of 714 c.c. in July to 236 c.c. in October in the northeastern sector, and from an average of 743 c.c. in June to 231 c.c. in October in the southern. In fact, only one of the stations yielded as much as 500 c.c. in that month. The contrast between the richer and the poorer catches on the offshore part of the shelf (the inshore belt was not sampled), was, however, no less striking in October (richest haul about 20 times the poorest) than it had been in the preceding summer (richest about 14 times the poorest). Hence, great irregularity of quantitative distribution appears to be as characteristic of a population that is (or recently has been) declining, as of one that is increasing, or near its maximum.

The only year (1916) in which towing was done in late autumn, was one when the summer plankton seems to have been more than usually abundant, following tardy vernal warming and consequent low summer temperatures. It appears from the original notes on the horizontal catches made by the late William Welch (no vertical or oblique tows were made) that the inshore waters still supported considerable amounts of plankton of one sort or another in that November, for "rich" catches were recorded locally on the inner half of the shelf south of Martha's Vineyard, close to Delaware Bay, and close in to Chesapeake Bay, contrasting, however, with only "fair" to "scanty" catches near the outer edge of the shelf all along from the offing of Martha's Vineyard to that of Chesapeake Bay. So far as these data go, in combination with those for 1931, they point toward a comparatively stable state for the last half of autumn.

There are no quantitative data for December or January, but it is likely that these months, and perhaps early February, see a progressive impoverishment in most years, especially in the northern half of the area, leading to the barrenness prevailing at the end of the winter. But considerable production may

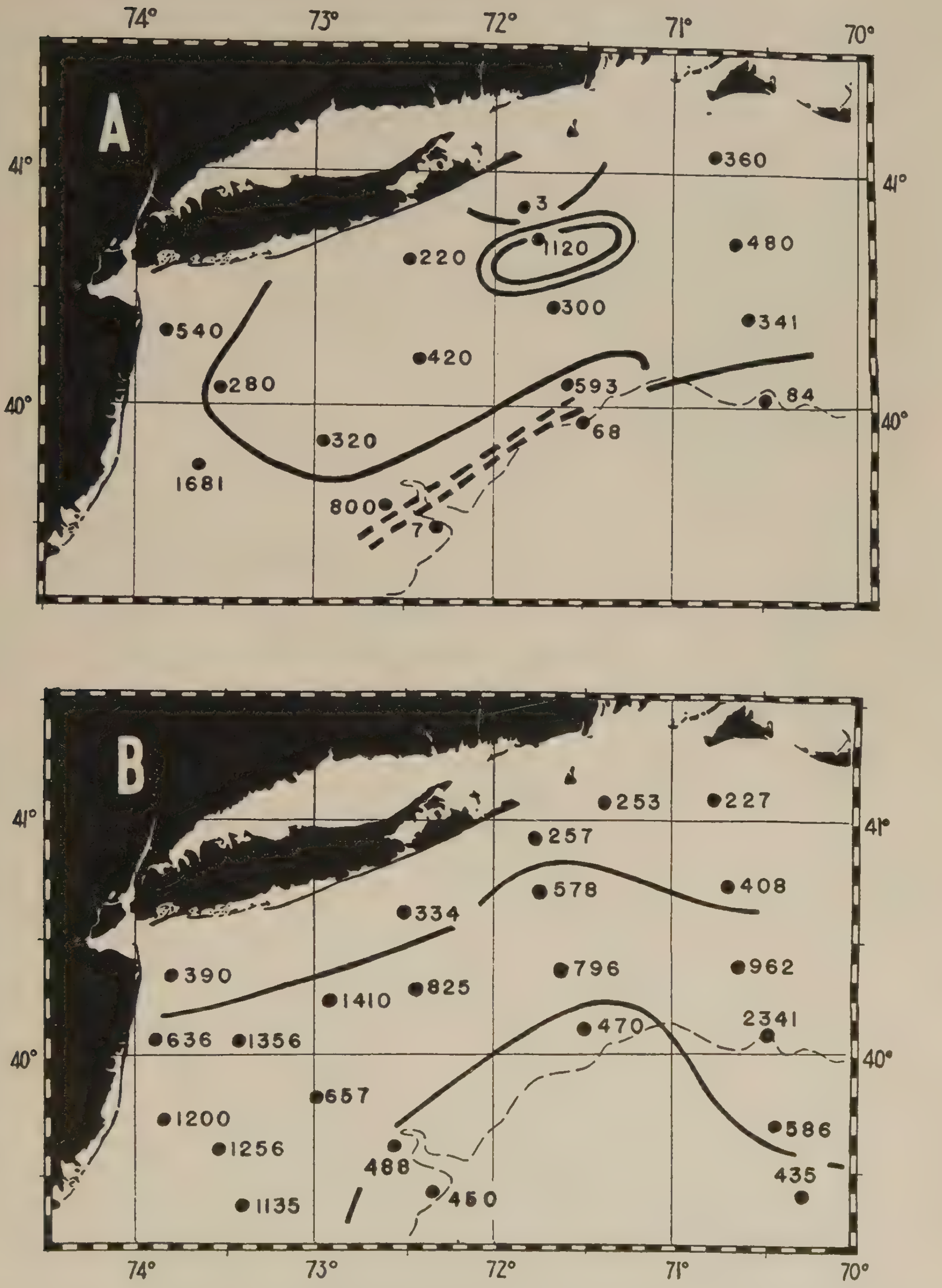

74°
73°
72°
71°
70°
A
41°
40°
360
3
1120
220
480
300
341
540
420
280
593
84
68
320
1681
800
7
B
41°
40°
253
227
257
578
408
334
390
962
796
825
1410
2341
470
636
1356
657
586
1200
1256
488
435
1135
450
74°
73°
72°
71°
70°

Fig. 8. Volumes of plankton, per standard haul, contour lines 100, 500, 1000 c.c.:–A, July 10–18, 1930; B, July 10–16, 1931.

take place in the southernmost sector in a normal February, judging from the fact that the center of abundance lies inshore and to the south in that month, as described above (p. 201), and the probability of this is especially strong in warm winters, to judge from the volumes that were recorded in February 1932 (p. 200).

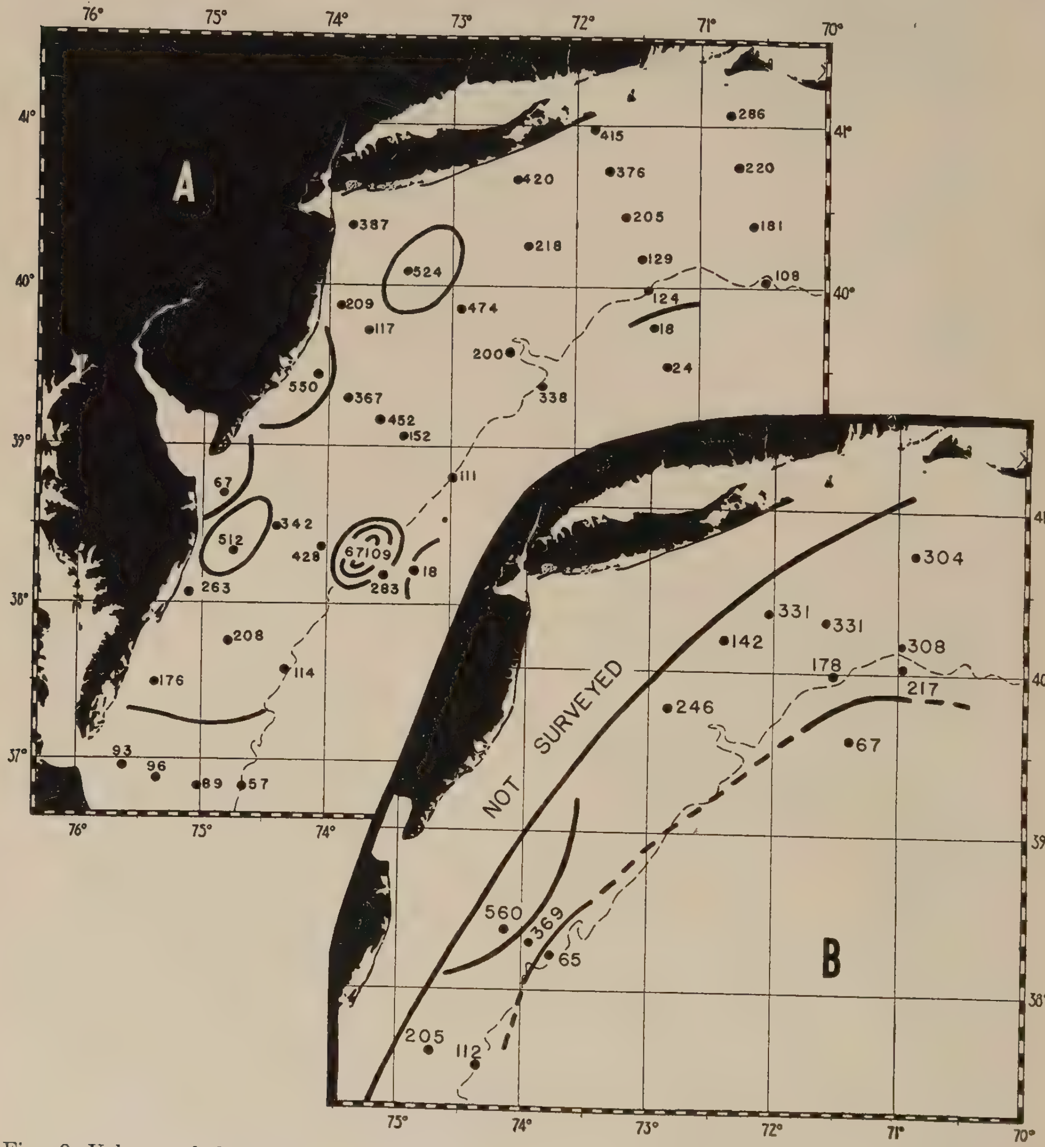

76°
75°
74°
73°
72°
71°
70°
41°
40°
39°
38°
37°
A
286
415
376
220
420
205
181
387
218
129
524
108
124
209
474
117
18
200
24
550
338
367
452
152
111
67
342
512
428
67109
283
18
263
208
114
176
93
96
89
57
B
304
331
331
142
308
178
217
246
67
NOT SURVEYED
560
369
65
205
112

Fig. 9. Volumes of plankton, per standard haul, contours 100, 500, 1000, 50000 c.c.: A, July 11–August 1, 1929; B, October 19–28, 1931, as calculated from vertical tows.

Annual Differences

In February, the plankton was decidedly more abundant in the southern sector after the warm winter of 1932 (average, 472 c.c., maximum, 2400 c.c., Fig. 2B), than in either 1930 or 1931 (average, 175–200 c.c., maximum, 1000 c.c.) which were much alike in this respect. Whether this means that more animals survived the preceding months in 1932, than usual, on account of the abnormally high temperatures of that winter, or whether vernal augmentation had already started at the time of that February survey is an open question. However, we may take 1932 as an example of the extreme in the variation to be expected in the one direction, i.e., in a February of extraordinary abundance. We might perhaps expect the other extreme—a great paucity—after an unusually severe winter. Unfortunately, data are lacking here, for while 1929 was the coldest February for which we have a complete temperature survey (Bigelow, 1933), no contemporaneous plankton tows were made.

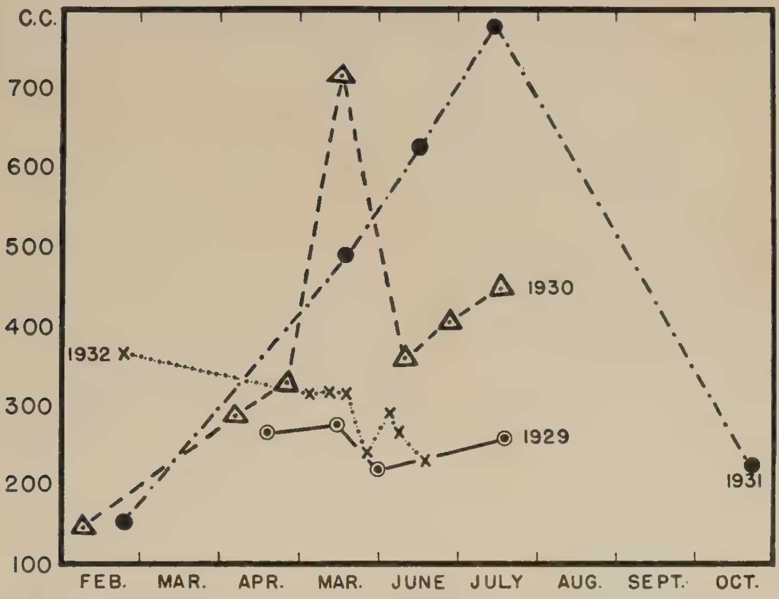


Fig. 10. Average volumes of plankton, for the area as a whole, in different months, for the several years.

The most interesting aspects of the annual comparison for spring and summer (Fig. 10) are that vernal augmentation was most pronounced, and summer volumes consequently greatest, in a year (1931) when the amount of plankton had averaged relatively small at the end of the winter, whereas there was no general augmentation of the plankton during the spring in the year (1932) when volumes had averaged largest in February: on the contrary, a slight impoverishment. But the facts that vernal augmentation was certainly of no great magnitude in 1929 either, following a cold winter (summer volumes consequently low), and that the positive anomaly of temperature existing in February 1932 had been entirely obliterated by that May, forbids our invoking temperature to explain year to year differences of this sort, unless the causes lie in conditions prevailing some time earlier in the season.

According to present information, the plankton as a whole may be expected to average about twice as voluminous, in our area, in a rich year as in a poor, at the end of the winter, a difference increasing to about 3 to 1 by midsummer.

Quantitative data, for the summers of 1913 and 1916, are not sufficient for inclusion in the preceding comparison, though the qualitative pictures for these two years are of much interest as representative of a warm and of a cold summer respectively.

Vertical Distribution

Studies of the vertical distribution of a mixed population are complicated by the fact that the existing state may depend on the precise proportions in which different species may enter into the general stock at any particular time and place. A case in point is the antithetical influence that would be exerted by a preponderance of Centropages, which usually has its center of abundance near the surface (p. 324) as contrasted with a preponderance of Calanus, which, through much of the year, is most abundant some distance below the surface (p. 310). We have also to distinguish between two categories of stratification that may be largely independent, first, that which results from diurnal vertical migrations, and second, what we name the "residual" stratification upon which the diurnal is superimposed. For the sake of clarity, it seems desirable to consider these two types separately.

Diurnal Stratification

The volumetric ratio of deep catch to shoal has varied widely from place to place on every cruise, by day as well as by night, depending largely on the precise qualitative composition of the community. In February, for example, of 1932—the only year, when hauls were made at two levels in that month,—the ratio of deep catch (22–24 meters) to shoal (7 meters) was about 0.3 to 1 at 3 A.M. on the 12th, midway out on the shelf off Cape May, where Euthemisto and Paracalanus jointly constituted 43% of the catch, but about 1 to 1 at midnight on the 26th, at about the same relative position off Bodie Island, where *Metridia lucens* was the leading species (38%). But the ratio, deep volume to shoal, averaged nearly the same between 8 A.M. and 4 P.M. (0.9 to 1, 5 cases) as between 8 P.M. and 4 A.M. (0.7 to 1, 8 cases), for that cruise as a whole. Evidently diurnal migration does not assume mass proportions at this time of year, either because the particular species concerned do not show this type of phototropic response on a broad scale, under the conditions of illumination then existing, or because the effects are then nullified by turbulent movements of the water.

But this ratio averaged significantly larger, however, during the hours of high illumination than during those of low, on each of the pertinent cruises for April, May, and June, as follows:

Average ratio of subsurface volume to surface volume,
day and night, 1929

April; 8 A.M.–4 P.M., 12–30 M., 28.8 to 1, 5 cases; 31–70 M., 1.4 to 1, 6 cases.
8 P.M.–4 A.M., 12–30 M., 1.2 to 1, 9 cases; 31–70 M., 0.6 to 1, 5 cases.
May; 8 A.M.–4 P.M., 12–30 M., 9.2 to 1, 4 cases; 39–64 M., 3.2 to 1, 3 cases.
8 P.M.–4 A.M., 12–30 M., 1.2 to 1, 4 cases; 39–64 M., 1.0 to 1, 2 cases.
June; 8 A.M.–4 P.M., 12–30 M., 5.5 to 1, 11 cases; 34–71 M., 2.4 to 1, 7 cases.
8 P.M.–4 A.M., 12–30 M., 1.9 to 1, 15 cases; 34–71 M., 3.9 to 1, 5 cases.

Average ratio of deep (> 20 meters) volumes to shoal (5–10 meters),
day and night, 1931 and 1932

1931, May; 8 A.M.–4 P.M., 19–32 M., 10.9 to 1, 7 cases; 39–64 M., 3.2 to 1, 3 cases.
8 P.M.–4 A.M., 19–32 M., 2.1 to 1, 5 cases; 39–64 M., 1 to 1, 2 cases.
June; 8 A.M.–4 P.M., 22 M., 6.8 to 1, 12 cases; 39 M., 7.4 to 1, 6 cases.
8 P.M.–4 A.M., 22 M., 2.0 to 1, 11 cases; 39 M., 1.6 to 1, 2 cases.
1932, May; 8 A.M.–4 P.M., 17–36 M., 1.4 to 1, 17 cases.
8 P.M.–4 A.M., 17–36 M., 0.9 to 1, 30 cases.
June; 8 A.M.–4 P.M., 20–28 M., 20.5 to 1, 14 cases.
8 P.M.–4 A.M., 20–28 M., 1.1 to 1, 22 cases.

Combination of the foregoing shows the ratio of volumes at, say, 18–36 meters, relative to that at 10–0 meters, to have averaged about 10.4 to 1 by day (37 cases) contrasted with 1.0 to 1 by night,[1] for April and May as a whole. Thus it is evidently characteristic of our area and of the particular assemblage of planktonic animals there existing, that diurnal migrations do attain sufficient magnitude during spring and early summer, to cause considerable enrichment of the mid-depths by day, at the expense of the surface stratum, the stratification that is temporarily built up in that way, being largely obliterated by night.

But the day-night contrast was usually much narrower at depths greater than 35 meters than in the mid-strata. In fact, no sign of diurnal alteration in this respect was recorded at 35 meters at the one station, where successive hauls were made several hours apart, though it was well marked at 20 meters and at 10 meters. Hence, we hazard the guess that diurnal migrations do not significantly affect the mass distribution of the plankton much below 40 meters depth.

---

[1] Meaning by "day," 8 A.M.–4 P.M., and by "night," 8 P.M.–4 A.M.

Diurnal stratification, though still widespread, is much less pronounced in June, to judge from an average ratio, deep catch to shoal, of about 3.8 to 1 by day and of 2.2 to 1 by night (47 cases) for that month in 1929, 1931, and 1932 combined, while on one of the cruises (June 1929) a contrast of the opposite order was recorded for the 39–64 meter level. And the difference in this respect, between the hours of strong illumination and weak, averaged still smaller in July, as follows:

Ratio of deep to surface volumes,[1] July 1929

8 A.M.–4 P.M., 10–30 M., 8.3 to 1, 7 cases; 30–60 M., 4.0 to 1, 6 cases; > 60 M., 3.3 to 1, 3 cases.
8 P.M.–4 A.M., 10–30 M., 7.8 to 1, 5 cases; 30–60 M., 3.2 to 1, 3 cases; > 60 M., 2.0 to 1, 4 cases.

Ratio of deep volumes to those at 7–10 meters, July 1931

8 A.M.–4 P.M., 20–30 M., 5.8 to 1, 4 cases.
8 P.M.–4 A.M., 20–30 M., 4.8 to 1, 5 cases.

But these July ratios, being consistently larger by day than by night, show that diurnal migration is a factor to be taken into account, even at this time of year, though its effects appear then to be strongly opposed by the vertical distribution of temperature (p. 219), at least for the particular assemblage of species with which we are concerned.

We have no information as to diurnal migrations, for autumn, or early winter.

The physical factors most obviously to be considered, in connection with vernal intensification of diurnal migration as a mass phenomenon, followed by weakening, in midsummer, are (1) increasing vertical stability of the water column, (2) the intensity of illumination, and (3) vernal warming of the surface. During the winter, and first two months of spring, when temperature and salinity are close to uniform from surface to bottom, over our area as a whole, the water has no significant vertical stability. And the vertical turbulence is evidently active enough to counteract any general tendency that may exist for the planktonic community to carry out diurnal migrations through February, when illumination is still relatively weak. In short, the plankton, like the other characteristics of the water, is kept thoroughly stirred, down to a depth of about 30 meters. In this connection, we should perhaps remind the reader that vertical stability influences the vertical distribution of the planktonic community chiefly by its control of vertical circulation, for the vertical gradient of specific gravity is not great enough, even when the water is most stable, seriously to affect the rate of vertical swimming for active organisms, or the rate of sinking, for passive.

---

[1] The tabulation is confined to the groups in which there were at least three cases.

It seems probable that the development of diurnal migrations on a mass scale by April, in spite of the fact that vertical stability still continues negligible, and vertical stirring consequently active, results from the increasing stimulus to phototropic response provided by the increasing intensity of illumination. Then, as the season advances, the vernal warming from above, combined with some decrease in the salinity of the surface waters (Bigelow, 1933; Bigelow and Sears, 1935) progressively renders the water column so much more stable that a corresponding frictional force (wind or current) would produce only about 1/3 as active stirring in the upper 40 meters of our area, as a whole, in June, and 1/8 as active in July as it would in mid-May[1]. The mechanical barrier to effective vertical swimming, thus breaks down in the stratum within which it was previously strongest. The positive phototropic stimulus to diurnal migration also continues to strengthen, during the late spring and early summer, as the intensity of illumination and the length of day increase, with increasing declination of the sun. These factors in combination, offer a reasonable explanation for the fact that diurnal migrations have proved to have much more effect on the vertica distribution of the planktonic community in April, May, and June, than in February. And the evidence discussed on page 219, indicates that its decline, as a mass phenomenon from June to July is due to the barrier to upward swimming imposed by the high temperature to which the surface warms in midsummer.

VERTICAL STRATIFICATION OTHER THAN DIURNAL

In February, the oblique tows made in 1932, at the groups of stations where two or more levels were sampled, yielded volumes averaging about as large at 20–27 meters (average, 267 c.c.) as at 3–8 meters (average, 251 c.c.), but only 13% as large at 39–49 meters (35 c.c.). And the vertical gradient is still stronger if the one richest catch for each depth-category, be omitted from the calculation. Nor was there any apparent evidence of any mass effects, by diurnal migration, in that month (p. 214). It thus appears that while some of the February stations showed one stratum considerably the more productive, and other stations the other, the plankton, on the whole, was distributed nearly uniformly, down to about 25–30 meters, but that it averaged less than one fourth as abundant in deeper water, a state probably reflecting the dominance of the community by Centropages and by Limacina at this season, and the prevailing scarcity of Calanus (p. 305).

---

[1] Calculations by C. O'D. Iselin.

But the center of population evidently tends to sink some 20–30 meters below the surface by early spring, there to continue until early summer, for the catches averaged 3 to 15 times as large from hauls centering at 12–30 meters as from those centering shoaler than 10 meters, in six of the seven cruises of record, April–June,—the one exception being May 1932, when the volume of plankton averaged about the same at the one level as at the other. And the fact that the ratio of average volume at 20–30 meters to volume at 10 meters or shoaler averaged 10.5 to 1 in July 1929, and 25.7 to 1 in that month of 1931, contrasting with about 3.8 to 1 for May and about 3.1 to 1 for June (all cruises combined) is evidence that concentration of plankton in the mid-depths tends to become still more pronounced as summer advances. It, also, appears that this enrichment, relative to the superficial stratum, likewise tends to extend to the deepest water on the shelf from June to July—though in lesser degree—for the ratio of volume at depths greater than 60 meters to those at the surface rose from 1.3 to 1 in May, and 1.9 to 1 in June, to 3.6 to 1 in July, in the one year (1929) when pertinent data were obtained.

It seems certain that the type of stratification, described above, is not the result of diurnal migration—general though that phenomenon be from April on—, because the observational series for April, May, and June includes a smaller number (70) of day time hauls, that would tend to magnify the effects of such migrations, than of night hauls (104) that would tend to obscure them, while the picture for July includes about as many hauls of the one category as of the other (11 day, 10 night). Neither can the initiation of vertical stratification of plankton be credited to temperature, for while this factor seems of great importance later in the season (p. 219), enrichment of the mid-level relative to the surface is established early in the spring, i.e., long before the upper strata have warmed to a value that could be considered unfavorable for the species concerned. An alteration in the qualitative composition of the plankton, does, however, offer a reasonable explanation, for while the community was dominated in the one February of record by Limacina and Centropages (combined, 67%), species that are usually most abundant near the surface, they have, on the average, been greatly surpassed, from April through July, by *Calanus finmarchicus* and *Sagitta elegans*, both of which average most abundant at mid-depths, as illustrated by the following tabulation, for the cruises on which hauls were made at two or more levels:

AVERAGE PERCENTAGE IN TOTAL CATCH

	Feb.	April	May	June	July
Centropages and Limacina	67%	13%	19%	11%	17%
Calanus finmarchicus and *Sagitta elegans*	2	68	43	55	64

Comparison between catches and temperatures at the mid-towing levels, argues strongly, however, that the progressive warming of the surface is the factor chiefly responsible for the rather abrupt intensification of the vertical plankton gradient, with corresponding impoverishment of the surface locally, that takes place from June to July, as was, indeed, forecast long ago, by the relationship between the stratum of chief abundance of Calanus and the temperature (Bigelow, 1922).

The fact that the majority of the dominant species are boreal, not arctic, would make it unlikely that any thermal control of vertical distribution would become operative until the surface had warmed above, say, 14°, nor do the data yield any suggestion of it in April or May, except perhaps at two stations close to the southern boundary of the area, where (in 1929) volumes were twice and eleven times as great at 15–30 meters, as at the surface, in temperatures of 17.8°–18.6°. The catches continued, in fact, to average nearly as large from one temperature as from another, through June, in one of the years (1932) when subsurface readings were obtained in that month — perhaps because of the scarcity of Calanus — although the surface had already warmed above 16° over considerable areas. A negative correlation had, however, developed by June between average catch and temperature, in the other pertinent year (1931), though with wide irregularity from station to station, as appears from the following tabulation.

	<12°	12.1°—16°	>16°
June 1931	903 c. c. 38 cases	322 c. c. 11 cases	313 c. c. 4 cases
June 1932	302 c. c. 46 cases	225 c. c. 28 cases	251 c. c. 14 cases

And the limitation of plankton by high temperature (again independent of depth) proved more obvious by July in each of the two years (1929, 1931) when tows were made at two levels in that month as follows:

	<12°	12.1°–16°	16°–18°	18°–20°	>20°
July 1929	383 c. c. 23 cases	485 c. c. 8 cases	—	149 c. c. 16 cases	77 c. c. 24 cases
July 1931	1025 c. c. 21 cases	664 c. c. 3 cases	280 c. c. 4 cases	127 c. c. 7 cases	197 c. c. 3 cases

Similar evidence lies in the fact that 7 out of 8 catches of 1000 c.c. for July 1931 were in hauls where the temperature at the mid-towing level was lower than 11° and none where it was warmer than 14°. It seems definitely established, therefore, that temperature and not depth *per se,* nor illumination (which is about the same in July as in June) is the factor responsible for the fact that the colder levels average several times as productive of zooplankton in midsummer as the warmer.

The thermal contrast between July, on the one hand, and May–June, on the other, consists not only in higher surface temperature, but also in the development of a more pronounced thermocline, raising the question whether the latter be significant in the present connection, or whether we have simply to do with the relative suitability of different temperatures for the particular species concerned.

Unfortunately, a definite answer cannot be expected from available data, because it seldom happened that the one haul was made just above the thermocline, and the other just below it, the picture being especially obscure for 1929, when the vertical intervals between hauls were, as a rule, broad enough to include both the thermocline and a considerable column of water within which the vertical gradient of temperature was small. The following comparison between the vertical gradient for temperature per unit depth and the ratio of shoal catch to deep, at stations (1929 and 1931 combined) where the depth intervals between the midpoints of successive hauls were not greater than 30 meters, might, it is true, suggest a very strong positive correlation between the two, if taken by itself.

Temperature difference per 10 meter depth	Average ratio of shoaler catch to next deeper	Extreme ratios	Cases
0–2°	1 to 3.4	1 to 0.5; 1 to 22.6	9
2.1–4°	1 to 2.6	1 to 0.5; 1 to 9.0	10
4.1–6°	1 to 18.6	1 to 0.4; 1 to 142.1	12
6.1–8°	1 to 41.4	1 to 4.8; 1 to 140.1	4

But it happened that the deeper haul was either made in water colder than 17°, or the shoaler in water warmer than 12°, wherever the thermal gradient per 10 meters was greater than 4°. In other words, either the one catch was made within the thermal range which appears most favorable for boreal plankton, or the other was made at a temperature that is much less so. In short, it is doubtful whether the steepness of the thermal gradient, *per se*, is of any importance in the distributional picture now under discussion.

The fact that the boreal plankton remains on the whole so definitely concentrated in the cooler part of the water column at the season when the surface is warmest, in spite of the widespread tendency toward diurnal migration, introduces interesting speculations as to the physiological mechanisms and responses involved—phototropism, geotropism (both of these perhaps being reversible by temperature), and also the possibility that such animals as Calanus, etc., may simply become immobilized at a temperature unfavorably high, and thus passively sink down again, to a more favorable environment.

We have no information as to vertical distribution for the community as a whole, for the autumn or early winter.

COMPARISON WITH OTHER AREAS

The great majority of zooplankton studies that have appeared during the last quarter century have been based on the enumeration of individuals, and when measurements have been made of the volumes of plankton present, these have in most cases been only incidental to the main thesis of the particular investigation in hand. For example, the only systematic records of volumes of zooplankton as distinct from phytoplankton that are included in the extensive lists of collections made by the Fisheries Services of the various North European countries in different years between 1902–1912, published by the International Council for the Exploration of the Sea in their several series of bulletins, are those contributed by the Swedish Fisheries Service for the Skagerak and for the Baltic (Conseil Permanent International pour l'Exploration de la Mer, 1904–1907). And it is obvious that there can be no basis for comparison between volumetric studies and numerical, unless one or the other includes some indication as to the relationship between the number of individuals and their volumes.

It is perhaps somewhat astonishing that such should be the case, because a majority of the campaigns of towing have received their impetus from fisheries investigations, from which standpoint, it would seem perhaps not less important to know the mass of animal plankton present than to know the number of individual animals making up that mass—at least if the point at issue be the foodstuffs available for fishes.

The result has been that while a vast body of information has been accumulated about life histories of the species of planktonic animals that are the most numerous in northern seas and the most important there as food for herring or other fishes, about the variations in their populations in space and time, and about their community associations, we still have only the haziest ideas as to the mass of animal substance that is characteristic of any part of the sea, at any depth, at any time of year—and even less idea as to how much may be produced annually. In this respect, the study of the zooplankton has lagged far behind that of the phytoplankton.

We also face the further difficulty that only a rough comparison is possible in most cases, even between different studies primarily volumetric, because of differences in the methods of collection and in the precision with which necessary information as to towing speeds, etc., has been presented. For example, the coarse nets used on the "Thor" and "Dana" expeditions (Jespersen, 1917, 1923, 1935), adequately sample only the larger planktonic animals such as are more abundant on the high seas, but fail for everything smaller than the largest copepods, i.e., for many of the species that are often predominant inshore, as illustrated by the fact that catches with a 2-meter stramin net, at eight of our own stations in June 1932, averaged only about 1/6 as voluminous as those made at the same stations with the silk net, when reduced to a common standard. On the other hand, fine meshed nets (#20 silk, 173 meshes per linear inch), such as have often been employed in quantitative studies, fail for the larger animals, but yield a combined catch of smaller zooplankton and of phytoplankton. Hence, catches made in them very seldom give a measure of the total animal fraction of the planktonic community, as distinct from the vegetable fraction.

Consequently, the allowances that must be made for divergences in procedure limit to the roughest such comparisons as we are able to make between our area and others where the volume of animal plankton has been recorded.

The following tables, summarizing the more extensive of the volumetric measurements of the zooplanktonic community as a whole, that have been made off the east coast of North America and off the northwestern coasts of Europe, are here expressed arbitrarily as cubic centimeters per cubic meter of water, rather than per unit tow, in the hope of giving the reader a more graphic picture (for a discussion of the methods of expression, see p. 197).

Volume of Plankton along the east coast of North America and West Greenland

Locality	Season	Authority	Settlement (S), or Displacement (D)	Calculated average, c. c. per cubic meter	Estimated c. c. per cu. meter by displacement
Cape Cod to Chesapeake Bay	Feb., 1930–1932 Apr., 1929–1930 May, 1929–1932 June, 1929–1932 July, 1929–1931 Oct., 1931		D	0.4 0.5 0.8 0.7 0.8 0.4	0.4 0.5 0.8 0.7 0.8 0.4
Martha's Vineyard	Sept.-Oct., 1935 Nov.-Dec., 1935 Jan.-Mar., 1936 Apr.-June, 1936 July-Aug., 1936	Clarke and Zinn (1937)	S	0.08 1.4 1.9 0.24 0.19	0.04 0.7 0.9 0.12 0.09
Gulf of Maine	July-Aug., 1913, 1916 March, 1920	Bigelow (1926)	S	0.7 0.4	0.35 0.2
	April, 1932 May, 1932 June, 1932 Aug.-Sept., 1932	Fish and Johnson [1] (1937)	D	0.7 0.34 0.21 0.16	0.7 0.34 0.21 0.16
	September, 1933 October, 1933 December, 1933 January, 1934 March, 1934 April-May, 1934 May-June, 1934 June-July, 1934 September, 1934	Redfield (unpublished data)	D	0.21 0.13 0.17 0.12 0.05 0.16 0.26 0.32 0.5	0.21 0.13 0.17 0.12 0.05 0.16 0.26 0.32 0.5
Bay of Fundy	April, 1932 May, 1932 June, 1932 Aug.-Sept., 1932	Fish and Johnson (1937)	D	0.04 0.19 0.2 0.09	0.04 0.19 0.2 0.09
Nova Scotia, Newfoundland Shelf	May, 1915 June, 1915 July, 1915	Huntsman (1919)	S	0.9 0.5 0.6	0.45 0.25 0.3
Gulf of St. Lawrence	May-June, 1915 August, 1915	Huntsman (1919)	S	0.5 0.5	0.25 0.25
West Greenland	August, 1924	Størmer [2] (1929)		0.35	0.17

[1] Dr. Fish informs us that the towing speed was very nearly 1.5 miles per hour.

[2] Stas. 32–63, 250–0 meters.

These series are all comparable with our own data, in that phytoplankton does not enter into the resultant volumes in more than minimal proportions. And the number of observations on which the average is based is large enough in each case for results to appear significant. But, in some cases, the measurement was by "settlement," which yields results averaging more than twice as large as does the "displacement" method. If allowance be made for this difference in method, the tabulation suggests that there is but little latitudinal difference, in the richness of plankton from the offing of Chesapeake Bay northward to the Gulf of Maine, in late winter or in early spring, when the zooplankton (near its yearly minimum for the continental shelf as a whole) averages only about 0.2–0.3 c.c. per cubic meter. But from May through July, the catches have averaged at least twice as large west and south from Cape Cod (about 0.6–0.7 c.c. per cubic meter) as for the Gulf of Maine (including the Bay of Fundy), for eastern Canadian waters, or for West Greenland, with the sector between Cape Cod and Delaware Bay averaging somewhat the richest of all, at the season of maximum abundance; the Bay of Fundy, and the Gulf of St. Lawrence somewhat the poorest.

The largest volume per cubic meter, as yet actually recorded from American waters is 116.1 c.c., at the edge of the continental shelf off Delaware Bay on July 18, 1929. But this—being the product of a local swarm of salpae—cannot be regarded as representative of more than the actual column of water fished. No doubt, a net drawn through one of the windrows of Aurellia, for example,—that are so commonly encountered in northern seas in summer—would yield a catch as large or larger. Aside from this (which may well have been equalled on many unrecorded occasions elsewhere), the maximum is 6.9 c.c. per cubic meter, in the offing of New Jersey, May 20, 1930. The Gulf of St. Lawrence ranks second in this respect, with 9.4 c.c. measured by the "settlement" method, equivalent to perhaps 4–5 c.c. by displacement (Huntsman, 1919), the Gulf of Maine third (4.3 c.c. per cubic meter by "settlement," or perhaps about 2 c.c. by displacement, Bigelow, 1926, Table, p. 94), while the maxima so far recorded for West Greenland and for the Scotian shelf are only 2.6 c.c. and 2.1 c.c., respectively by "settlement," corresponding to about 1 c.c. by displacement.

It has long been a matter of common knowledge that rich concentrations of plankton occur in summer in the upper water layers around Iceland. Assuming a towing speed of 1.5 knots, Damas' (1905, p. 15) record of a catch of more than 1000 c.c. of young Calanus alone in a five minute haul at the surface with a one meter net—frequently quoted as an instance of extraordinary abundance of

Volume of Plankton in North European Waters

Locality	Season	Authority	Settlement (S), Draining (Dr.), or Displacement (D).	Calculated average, c. c. per cubic meter	Estimated c. c. per cu. meter by displacement
Iceland	July, 1924	Størmer (1929)	S	0.4	0.2
Iceland, Faroes, Ireland		Jespersen (1923)	Dr.[1]	0.84	0.84
Southern Norwegian Sea	July-August, 1924	Størmer (1929)	S	0.6	0.3
North Sea	June, 1926 Aug., 1926 Nov., 1926	Savage (1931)	S	1.15 1.0 1.2	0.57 0.5 0.6
		Jesperson (1923)	Dr.[1]	0.013	0.013
English Channel	April, 1925 May, 1925 June, 1925 July, 1925 Aug., 1925	Russell (1927)[2]	S	0.03 0.20 0.04 0.11 0.10	0.01 0.10 0.02 0.05 0.05
Skagerak	Feb., 1903 Aug., 1903 Nov., 1903 May, 1904 Aug., 1904 Nov., 1904 Aug., 1906	Conseil permanent international pour l'exploration de la mer (1904–1907)	S	0.08 0.09 0.28 0.18 0.09 0.32 0.04	0.04 0.05 0.14 0.09 0.05 0.16 0.02
Baltic	Aug., 1903 Aug., 1904 Aug., 1906	Conseil permanent international pour l'exploration de la mer (1904–1907)	S	0.04 0.45 0.07	0.02 0.22 0.04
	May-June, 1931	Mielk and Künne (1935, p. 69)	S	0.95	0.5

plankton—corresponds to about 6 c.c. per cubic meter, if the volumetric measurement was made by displacement, which ranks with the richer catches in the Gulf of St. Lawrence, and south of New York. It is more impressive, in the present connection that the average of 0.84 c.c., for 82 "Thor" catches between Iceland, the Faroes, and Ireland (Jespersen, 1923, p. 4, Fig. 1; Schmidt, 1912, p. 8) may well have represented a community richer than any that has thus far been reported for any considerable area in the western Atlantic, most of the smaller copepods, etc., having very likely been lost through the coarse-meshed nets that were used. And while Størmer (1929) reported much smaller volumes from Icelandic waters (average, 0.4 c.c. per cubic meter, by settlement, or perhaps 0.2 c.c. by displacement) his measurements were made at two stations only, and after removing some of the more bulky forms (medusae, etc.).

---

[1] We have found by experiment that measurement by "draining" agrees closely with that by "displacement."

[2] We are informed by Dr. Russell that his towing speed was between 1.5 and 2 knots.

The average recorded by Størmer (1929) at 23 "Michael Sars" stations, in the southern part of the Norwegian Sea of about 0.6 c.c. per cubic meter, with a maximum for any one haul of about 3.4 c.c. per cubic meter, is about half that for our own area (p. 223), if allowance be made for the difference between measurements by "settlement" and by "displacement."

In the North Sea, many measurements of plankton volume, per cubic meter, were long ago made by Apstein (1906) and Kraefft (1910), yielding very large values. But their catches were made in such fine nets (173 meshes per linear inch) that the recorded volumes include the phytoplanktonic fraction, nor do the published data afford any way of estimating the volume of the zooplanktonic fraction, as distinct from the latter, and this applies equally to the volumes given for the Baltic and North Sea, by Mielck (1911), Lücke (1912), and Büse (1915). On the other hand, the very low average (corresponding to 0.013 c.c. per cubic meter) reported for the North Sea by Jespersen (1923, Fig. 1), may be chargeable—at least in part—to the very coarse mesh of his stramin nets. Volumes for the North Sea calculated from the lists more recently published by Savage, (1931, Tables 13–17), in connection with his studies of the food of the herring, agree closely with the summer average for our own area, when reduced to the "displacement" basis according to Savage's comparison of methods, though the maximum reported by him of 7 c.c. per cubic meter by "settlement" was somewhat lower.[1]

Zooplankton would appear to be considerably less abundant in the English Channel than in the North Sea, according to Russell's (1925, 1927) records. And Dr. Russell writes us that "the mixed oceanic and coastal water near the continental shelf is probably richer, and the English Channel and southern North Sea are rather poorer in plankton content" (quoted from a letter of January 28,

---

[1] For description of the type of net employed, see Cons. Int., Publ. Circ., No. 84.

1938), though this regional contrast may be not as wide as the calculated volumes indicate, because the nets used in the Channel would retain "only the more bulky of the planktonic organisms" (Russell, 1927). And the long series of vertical tows made by the Swedish Fisheries Service show a decided poverty in the Skagerak, as contrasted with the North Sea, with the English Channel, or with the coastal waters of northeastern America as a whole. But the volumes—chiefly copepods—reported for the western part of the Baltic by Mielck and Künne (1935, p. 69) correspond quite closely to the averages east of Great Britain, when reduced to a common standard (see Table, p. 225). And this also applied in two surveys out of three, to the region farther east and north in the Baltic examined by the Swedish cruises in August of 1903, 1904, and 1906.

The foregoing comparisons point to the waters between Iceland, the Faroes, and Scotland as probably somewhat more productive of zooplankton, at the season of chief abundance than is any other considerable sector of the boreal belt (including tributary seas), of the North Atlantic. In fact, it would not be astonishing if these waters should finally prove to support 4–6 times as large a volume of plankton, as does the most closely competing region, to judge from the allowance to be made for the size of mesh used in the nets. Next in rank, come the American sector between Cape Cod and Chesapeake Bay on the one side of the Atlantic, and the North Sea on the other, the former with an average of about 0.7–0.8 c.c. per cubic meter, at the peak season, as measured by displacement, the latter with 1.4–1.9 c.c., as measured by settlement, which corresponds to perhaps 0.5–0.6 c.c. by displacement. And it is further interesting that 1932 was a poor year for plankton in each of these areas, on opposite sides of the Atlantic (Savage, 1937). The Gulf of Maine and Scotian shelf in the west and the southern North Sea and Baltic in the east, similarly fall together at the season when the plankton is richest, but with somewhat smaller volumes, corresponding to about 0.2–0.4 c.c., or perhaps somewhat less, by displacement. But no attempt has been made to estimate the total yearly production (volumetric) of zooplankton for any part of the sea—so far as we are aware. And the relative ranking on this basis may differ widely from the foregoing, with Icelandic waters, where active production is probably confined to a short season, perhaps falling below our own waters and below the North Sea region.

The striking feature of the comparison is not the demonstrated diversity, i.e., that one boreal locality may average several times as rich as another, whether for the column of water as a whole on the continental shelf, or for the upper strata farther out to sea, but rather, that the average volumes for different regions, at the season of maximum abundance (Tables, pp. 223, 225), should differ so little, one from another, relative to the volume of water containing them. If allowance be made for the method of measurement and for the size of mesh, the extreme range is only from about 1 to about 8 volumes of animal plankton, of the size of medium-sized copepods and larger, per 10 million volumes of water, though individual catches may run as high as 1100 volumes or more (p. 224).

There would be little profit in extending the comparison farther afield, because the published records of volumetric abundance for other seas are based chiefly on catches made in nets either of mesh so fine that they retain the vegetable as well as the animal fraction, e.g., Hensen's (1890) study of volumetric distribution between Bermuda and the Cape Verdes, and Boschma's (1936), for the East Indies, or so coarse that they may have lost a considerable fraction of the stock of animals in some localities, but perhaps very little at others. We need merely remind the reader of Jespersen's (1923, 1924) well known demonstration, based on catches with very coarse (stramin) nets, of poverty in the Mediterranean and in the Sargasso Sea region, contrasted with richness in the northeastern Atlantic, and of his more recent comparison (1935, Fig. 27) between the upper water layers in various parts of the Atlantic and Pacific at mid- and low latitudes.

RELATIVE ABUNDANCE OF DIFFERENT SPECIES

Dominant species. Previous information (p. 192) had shown that the waters on the continental shelf more than a few miles out from the land, and from Cape Cod as far west as the offing of New York are dominated in late summer and autumn by much the same boreal communities—lead by *Calanus finmarchicus*—as characterize the Gulf of Maine to the eastward. And similar conditions had been found to extend southward at least to the latitude of Chesapeake Bay in a cool summer (illustrated by 1916), though in a warm one (e.g., 1913), the waters in this southern sector may be monopolized locally by swarms of neritic species of ctenophores, on the one hand, or of salpae (of oceanic origin), on the other, with a considerable variety of other warm oceanic visitors recorded here and there, though never in any significant volume.

The records for the period, 1929–1932, now add the information that the same boreal "Calanus" community similarly dominates our area as a whole, southward at least to Latitude 36° N., from the end of the winter, through spring and early summer, in the relative proportions tabulated below, and that immigrants from the warm oceanic community that constantly inhabit the waters along the continental edge, are no more important, volumetrically, on the shelf during the vernal half year than they are in summer or autumn.

Average Percentages in the Total Zooplankton of Species that have Formed 1% or more, by Volume, in any One of the Subdivisions

Date	Sector	C. finmarchicus	C. typicus	M. lucens	P. parvus	P. minutus	L. retroversa	S. elegans	S. serratodentata	E. compressa	Euphausiids	Ctenophores	A. digitale	Leptoline medusae	Crab larvae	O. labradoriensis	Salps	Doliolum	C. limacina	Oceanic copepods
Feb., 1930	Inshore	3	49	<1		6	<1	7	21	<1	1						<1			
	Offshore	10	2	12		7	8	4	20	2	20						2			
	North	9	11	4		6	4	17	31	<1	2						<1			
	South	1	59	1		7	<1	<1	14	<1	4						<1			
	Total area	5	41	4		7	2	6	20	1	3						<1			
1931	Inshore	13	<1	<1		2	<1	55	25	1										
	Offshore	28	11	21		8	<1	15	2	3										
	North	9	2	3		20	<1	51	1	1										
	South	16	5	10		2	<1	37	18	2										
	Total area	19	5	9		5	<1	38	15	2										
1932	Inshore	1	31	6	6	4	41	<1	3	1							<1			<1
	Offshore	1	6	15	19	<1	9	<1	18	9							2			3
	North	15	14	12	21	1	1	<1	3	12							<1			7
	South	1	29	7	6	1	41	<1	5	1							<1			2
	Total area	1	29	7	8	3	38	<1	5	2							<1			<1
April, 1929	Inshore	56	11	0		<1	9	5	12	<1	<1									
	Offshore	73	6	5		2	<1	<1	4	<1	2									
	North	73	6	4		2	4	3	<1	<1	2									
	South	58	12	1		<1	5	0	17	<1	<1									
	Total area	66	9	3		1	4	2	8	<1	1									
1930	Inshore	40	11	5		11	12	7	3	3	<1									
	Offshore	40	3	27		5	13	4	3	2	1									
	North	44	2	18		6	12	11	2	2	1									
	South	36	15	12		9	9	3	5	4	<1									
	Total area	41	7	16		8	6	8	3	2	<1									
May, 1929	Inshore	21	6	<1		<1	18	9	1	<1	8	25		1	2	1	0	0		
	Offshore	47	5	2		<1	6	10	3	<1	2	0		<1	<1	<1	1	1		
	North	41	4	1		<1	15	14	<1	<1	5	0		<1	<1	<1	1	0		
	South	18	8	1		<1	9	1	7	<1	1	46		2	3	<1	<1	2		
	Total area	33	5	1		<1	12	9	2	<1	4	13		<1	1	<1	<1	1		
1930	Inshore	35	5	2		<1	24	13	<1	5	<1		2		1					
	Offshore	25	1	6		<1	56	3	1	3	<1		<1		<1					
	North	38	1	8		<1	36	6	<1	3	<1		<1		<1					
	South	18	3	1		<1	55	8	<1	3	<1		1		<1					
	Total area	29	2	5		<1	45	7	1	4	<1		<1		<1					
1931	Inshore	30	<1	<1		7	12	34	<1	<1				8	<1	1				
	Offshore	69	<1	9		5	4	3	<1	<1				1	<1	1				
	North	61	<1	6		7	3	11	<1	<1				3	<1	1				
	South	24	<1	3		4	21	36	<1	<1				8	<1	1				
	Total area	52	<1	5		6	8	17	<1	<1				4	<1	1				
1932	Inshore	8	6	3		12	29	10	1	<1	<1		7	2	4	8	0		<1	<1
	Offshore	28	1	14		5	17	2	2	<1	7		1	<1	1	4	3		1	2
	North	21	3	10		6	25	4	1	<1	5		4	2	1	8	2		<1	<1
	South	10	15	6		11	21	2	2	<1	3		4	<1	5	3	1		1	2
	Total area	16	8	8		8	23	6	2	<1	4		4	1	3	6	1		1	1
June, 1929	Inshore	25	9	6		1	9	23	1	3	1			1	5	1	0		3	
	Offshore	46	4	9		<1	3	11	2	<1	6			0	1	1	9		1	
	North	43	2	4		1	6	22	<1	<1	6			1	3	1	5		1	
	South	17	16	6		<1	4	1	1	5	1			1	2	1	4		6	
	Total area	37	6	5		<1	5	18	1	1	5			1	2	1	3		1	
1930	Inshore	41	1	<1		<1	20	19	<1	9	<1		1	<1	1	<1	0		<1	
	Offshore	61	<1	7		<1	6	4	<1	3	2		<1	<1	<1	<1	<1		<1	
	North	57	<1	3		1	18	8	<1	5	1		1	<1	1	<1	<1		<1	
	South	17	<1	<1		<1	1	48	<1	17	<1		<1	<1	<1	<1	0		<1	
	Total area	52	<1	2		<1	15	13	<1	7	1		1	<1	1	<1	<1		<1	
1931	Inshore	59	2	1		6	1	25	<1	<1	<1		<1	1	2	<1	0		<1	
	Offshore	74	1	3		2	<1	11	2	<1	<1		<1	<1	<1	<1	1		<1	
	North	76	1	2		5	<1	9	1	<1	<1		<1	<1	2	<1	<1		<1	
	South	41	2	1		3	3	39	2	<1	<1		<1	<1	1	<1	0		1	
	Total area	65	1	2		4	1	17	1	<1	<1		<1	<1	1	<1	<1		<1	
1932	Inshore	8	14	2		4	6	14	<1	<1	2		28	2	2	<1	0		2	
	Offshore	26	7	12		3	12	4	2	1	6		6	<1	<1	<1	9		8	
	North	18	6	6		4	7	17	1	1	4		19	2	<1	<1	2		1	
	South	14	17	4		3	12	8	4	2	4		15	<1	<1	<1	8		9	
	Total area	16	11	6		3	9	12	2	1	4		17	1	2	<1	4		5	
July, 1929	Inshore	27	20	<1	1	<1	2	35	<1	1	1	<1		2	<1		0	1		<1
	Offshore	32	14	4	<1	<1	<1	21	3	1	6	4		<1	<1		7	3		3
	North	35	19	2	1	<1	1	28	1	1	3	<1		2	<1		3	0		<1
	South	9	13	<1	1	<1	2	36	2	2	<1	5		<1	1		1	5		4
	Total area	29	18	1	1	<1	1	30	1	1	2	2		1	1		2	1		2
1930	Inshore	47	35	<1		<1	3	7	<1	6	<1	<1		<1	<1		0			<1
	Offshore	69	3	7		<1	4	5	<1	<1	<1	<1		0	<1		<1			<1
	North	57	20	3		<1	3	6	<1	6	<1	<1		<1	<1		<1			<1
1931	Inshore	57	20	<1		3	3	6	<1	<1	<1	<1		3	<1		0			<1
	Offshore	64	1	<1		1	0	2	<1	<1	<1	<1		<1	<1		24			<1
	North	61	12	<1		1	1	4	<1	<1	<1	<1		1	<1		11			<1
Oct., 1931	Offshore	7	34	7	17	2	<1	5	5	<1	<1						<1			5
	North	8	47	11	26	1	<1	3	2	<1	<1						0			1
	South	7	14	2	12	4	<1	7	9	<1	<1						1			12

Monthly Succession

February. The only species that have averaged more than 1% (by volume) of the total catches, in any one of the years, for the region as a whole, in February are the following:—*Calanus finmarchicus, Centropages typicus, Euthemisto compressa, Limacina retroversa, Metridia lucens, Paracalanus parvus, Pseudocalanus minutus, Sagitta elegans,* and *Sagitta serratodentata.* Combined, these have constituted from 86% to 94%, by volume, of the winter catches. In no instance, in fact, was as much as 50 c.c. of any other species taken at any of the February stations.

The tabulation (p. 229) of relative percentages shows that in a given year, either *Centropages typicus, Sagitta elegans,* or *Limacina retroversa* may be the leading species at this season. As a rule, this applies, also, for individual localities where rich (> 300 c.c.) catches were made, the only notable exception, being for one station, where *Sagitta serratodentata* ranked high. *Calanus finmarchicus* (dominant later in the season) occupies a minor, or at most an intermediate position inshore at the end of winter, ranking fifth there, on the average, while offshore, it ranks second (next to Metridia). In February, Calanus has also averaged more important to the north of the Cape May profile (ranking third, for the three years combined), than southward (ranking fifth); so, too, Euthemisto. On the other hand, *Centropages typicus* was relatively much more important in the south than in the north, in the two years when it occurred in significant proportion in either subdivision. In the cases of the other dominant species, the north-south relationships have been so irregular that no general rule can be derived from so short a series of observations.

The February list of dominant species includes no benthonic derivatives of any sort, no neritic larvae, no visitors from offshore; evidence that contributions from the coast line, and from the bottom beneath, on the one hand, or from the continental slope, on the other, are negligible.[1] Neither does it include any immigrants, whether from colder coastal waters to the north, or from warmer to the south.

But the following additional species have occasionally constituted 1%, or more, at individual stations in February, north of Latitude 36° N.:

> *Aglantha digitale,* 4 stations, 1–10 c.c., 1–7%; *Candacia armata,* 1 station, 27 c.c., 5%; *Centropages hamatus,* 1 station, 10 c.c., 1%; Crago sp., 2 stations, 4–22 c.c., 3–15%; cumaceans, 2 stations, 2–6 c.c., 1–4%; Eucalanus sp., 1 station, 2 c.c., 1%;

---

[1] Perhaps on account of failure regularly to sample close to bottom, see page 193.

Euphausia sp., 2 stations, 9 and 28 c.c., 9 and 32%; *Nematoscelis megalops*, 4 stations, 5–40 c.c., 25–81%; *Neomysis americana*, 1 station, 4 c.c., 2%; Oithona sp., 3 stations, 1–30 c.c., 1–2%; *Pleuromamma gracilis*, 5 stations, 4–15 c.c., 10–41%; *Rhincalanus nasutus*, 1 station, 9 c.c., 2%; salps, 2 stations, 11–17 c.c., 32–57%; *Thysanoessa inermis*, 1 station, 16 c.c., 3%.

The winter stations occupied in 1931, in the immediate vicinity of Cape Hatteras, show that the eight species which dominate to the northward of Latitude 36° N., are outclassed farther south, by species of oceanic origin, for while the former category constituted only 11–12% of the average catch there, Noctiluca formed 8%, *Sagitta enflata*, 11%, and oceanic copepods, 42%, with the remaining 34% consisting of a varied assemblage of oceanic decapods, amphipods, siphonophores, and medusae, among which some 51 species were identified.

April. The same species have not only dominated in April (Fig. 11B), as in February, but, in combination, they have formed about the same average proportion of the total catches (89–93%), for the area as a whole. And their combined importance is not appreciably affected by the entrance by April into the "dominant" category of a new member—euphausiids—for these were still in low percentage (1%) and counterbalanced by a decline on the part of Paracalanus. In fact, the seven leading species monopolized the large (> 500 c.c.) catches, even more strongly (80% in each of the 19 cases) in April than in February.

The most instructive feature of the lists for April, compared with February, of the one year (1930) when surveys were made in both, is that *Calanus finmarchicus* had increased so greatly, in relative importance, from the one month to the other as to make it by far the most prominant species in the northern sector, while in the southern sector, it was dominant at the time of the first April cruise of that year, and about equalled its closest rivals (Centropages and Pseudocalanus) at the time of the second. The area where Calanus averaged 20% or more of the total volume of plankton (confined to localities in the northeast in February) had also expanded by early April to cover the waters generally (though with local exceptions) down to the offing of Chesapeake Bay. And the fact that Calanus was present in even larger percentage in April of 1929 (when no information was obtained in February), than of 1930, is evidence that the seasonal sequence recorded in the latter year may be accepted as normal. This increase in Calanus was, in fact, chiefly responsible for the great augmentation of the plankton as a whole that took place in the early spring of 1930 (p. 203). And this statement applies not only to the region as a whole, but to individual localities as well, for wherever the total catch was much larger in that April, than it had been in the

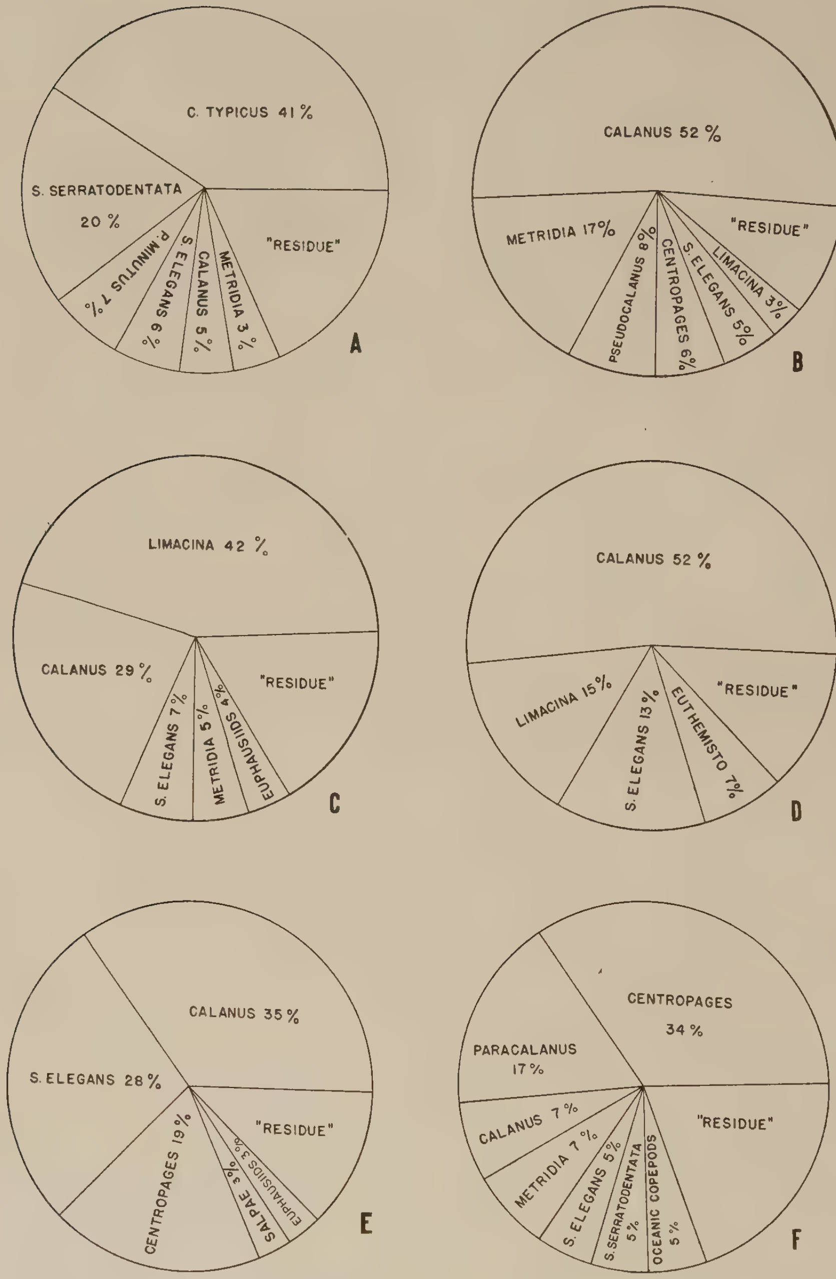


Fig. 11. Percentages (by volume) of dominant species in average catch for the area as a whole: A, February 5–13, 1930; B, April 3–11, 1930; C, May 12–23, 1930; D, June 7–18, 1930; E, July 11–August 1, 1929, and F, October 19–28, 1931.

preceding February, the percentage of Calanus was also much larger, whereas its percentage was higher in some cases, and lower in others at stations where little alteration had taken place in total volume.

It also deserves emphasis that Calanus—so far as can be judged from the rather unsatisfactory series—is the only member of the dominant group that usually experiences a great and general augmentation in relative abundance, within the confines of our area, in early spring. At the same time, it appears to be rather more common in April than in February—perhaps forecasting greater diversity in the general averages in May—for species other than the dominants, to form as much as 1% of the community, at individual stations, the recorded instances being:

Aglantha digitale, 4 stations, 2–10 c.c., 1–8%; amphipods, 4 stations, 3–22 c.c., 1–9%; annelid worms, 1 station, 47 c.c., 24%; *Anomalocera pattersoni*, 1 station, 1 c.c., 12%; *Candacia armata*, 1 station, 4 c.c., 3%; *Centropages hamatus*, 5 stations, 3–35 c.c., 1–15%; Corycaeus sp., 1 station, 2 c.c., 1%; decapod larvae, 6 stations, 2–82 c.c., 1–43%; euphausiid larvae, 17 stations, 3–60 c.c., 1–54%; *Eucalanus attenuatus*, 6 stations, 3–18 c.c., 1–29%; Euchaeta sp., 1 station, 2 c.c., 1%; *Euchirella rostrata*, 2 stations, 3–6 c.c., 2–3%; leptomedusae, 2 stations, 12–25 c.c., 21–21%; *Lucifer typus*, 1 station, 8 c.c., 7%; *Nematoscelis megalops*, 1 station, 23 c.c., 1%; *Oikopleura labradoriensis*, 1 station, 9 c.c., 3%; *Pleuromamma gracilis*, 2 stations, 2–9 c.c., 1–5%; *Rhincalanus nasutus*, 4 stations, 5–40 c.c., 4–30%; oceanic sagittae, 2 stations, 2–4 c.c., 1–2%; *Sagitta enflata*, 2 stations, 11–12 c.c., 10–10%; salps, 4 stations, 4–30 c.c., 4–27%; *Temora stylifera*, 2 stations, 4–7 c.c., 3–6%.

May. Calanus averaged about as important in the total community, for the area as a whole in May (30–50%) as in April (40–60%), in the years when the winter had been normally cool, i.e., 1929, 1930, 1931, but after a warm winter (1932), it was much less so (16%). In all years (1929–1932), however, it averaged much more important relatively in the offshore belt than inshore, though with considerable difference in this respect from year to year, and about twice as important in the north as in the south. On the other hand, while Calanus was the largest single item in April in both years of record, in May this was true in two years (1929, 1931) only, whereas in the other years (1930, 1932), it was surpassed by Limacina. And the percentage of Calanus in the rich ($>$ 500 c.c.) hauls also averaged considerably lower in May (16–27%) than it had in April (33–77%) in the two years (1929, 1930) for which information is available for both these months. Conflicting evidence of this sort is perhaps more reasonably explained as due to the brevity of the observational series, and to the roughness of the methods, than to any definitely seasonal trend, one way or the other, from the one month to the next.

Centropages, contrasting with Calanus, declined greatly in relative abundance, between February, or April, and May in three of the four years of record (1929, 1930, 1932), as appears from its average volumes and percentages for the area as a whole (Table, p. 229), while in the fourth year (1931), this species was so scarce throughout the season that the calculated monthly values are not significant for it in this connection. Furthermore, Centropages, which formed more than 50% of the catch at five out of eleven winter stations where more than 300 c.c. of plankton was taken, equalled 30% at only one of the 60 "rich" (> 500 c.c.) hauls for April and May combined.

Corresponding to this vernal decrease in relative importance, the area where Centropages averaged as much as 10% of the total volume contracted considerably in the north from February to April in 1930, though expanding offshore in the south meantime, while in 1932, a decided contraction of the same sort had in any case taken place by May, showing that this copepod is on the average, only a minor element(<1–5%) in the northern sector by the end of spring. And it is not much more important then, in the southern sector(<1–8%) in normal years (e.g., 1929, 1930), though after a very warm winter (as in 1932), its percentage may average but little lower in May (15%) than in February (29%). A vernal decline in relative importance seems equally characteristic of *Sagitta serratodentata*, judging from the fact that its percentage in the total catches averaged only about 1/20 as great in May as in February of 1930, less than 1/15 as great in 1931, and 1/5 as great in 1932. In fact, only two out of ten spring cruises showed it as forming as much as 2% of the general community (Table, p. 229). And it seems that it usually declines to less than 5% by May, even in the southern sector, where a considerable percentage of it may persist until April in some years (e.g., 1929, 16%).

The vernal histories of other members of the group that are dominant at the end of winter are less regular, for they may show increases in some years, decreases in others, though these alterations have usually been of a smaller order of magnitude than for Calanus, for Centropages, or for *Sagitta serratodentata*. In some years, for example, Pseudocalanus shows an upward trend at first, but then a decline, as in 1930, when its percentage about doubled between February and April, but then fell to an insignificant figure by May. And it may have experienced a similar succession in 1929, when it formed less than 1% in May (no information for that February). But the alteration was of the reverse order in 1932, when its percentage more than doubled between February and May, while in the fourth year of the series, its relative standing was about the same in the one month as in the other.

The vernal cycle for *Metridia lucens* seems to have paralleled that for Pseudocalanus in 1930, when its average percentage about quadrupled from February (4%) to April (16%), with a corresponding expansion of the area where it averaged as much as 10%, but then fell again by about 1/3 to May (5%). But it is doubtful whether any significant alteration in its relative abundance took place during the spring of 1929, of 1931, or of 1932, because its percentage in each of these years averaged about the same in May as it had in February. Neither is there any evidence that notably rich centers ever develop for Metridia at this time of year, as happens frequently for Calanus, and at least occasionally for Pseudocalanus. Metridia, however, continues as definitely an "offshore" species through the spring, as it is in February, its percentage having averaged about 2–17 times as high offshore as inshore, both in April, and in May of each year of record, also about twice as high in the north (8%) as in the south (4%) for the April-May cruises combined.

The year (1930) that saw the most pronounced fluctuations for Metridia was, however, one of comparative constancy from February through April to May, for *Sagitta elegans*. But the area where this chaetognath was relatively important (> 10%),—even less extensive early in that April than it had been in February—then greatly expanded southward by May. And in 1929, its percentage in the catches about quadrupled from April (2%; no February data available) to mid-May (9%). Likewise in 1932 it averaged more important in May (6%), than it had in the preceding February (1%), while in 1931 (thanks to more rapid multiplication by Calanus), it was in only about half as great percentage in the one month (17%) as it had been in the other (38%), although it had meantime increased in average abundance from about 58 c.c. to about 84 c.c. Regionally, however, the picture for *S. elegans* is more consistent than the foregoing might suggest, for in all years of record, it ranked considerably higher in percentage inshore (5–34%) than offshore (< 1–10%) in April and May, as seems in fact to be the general rule for it; also higher in the northern sector (3–14%) than in the southern (< 1–4%) on seven of the ten spring cruises.

In the case of Limacina, a 3-fold increase in percentage was registered between April (4%) and May (12%) in 1929, a 15-fold between early April (3%) and mid-May (45%) in 1930, and an 8-fold between February (< 1%) and May (8%) in 1931, with corresponding wide southward expansion of the areas where it averaged as much as 10% of the total community (Fig. 12). On the other hand, its percentage decreased by nearly ½ between February (38%) and May (23%) in 1932 (all stations combined). Neither has the north-south or inshore-offshore relationship of Limacina proved any more consistent at this season, its percentage having averaged at least ½ greater in the north than south on four of the ten spring cruises, but the reverse on two others, and significantly greater inshore than offshore on five cruises, but greater offshore than inshore on two.

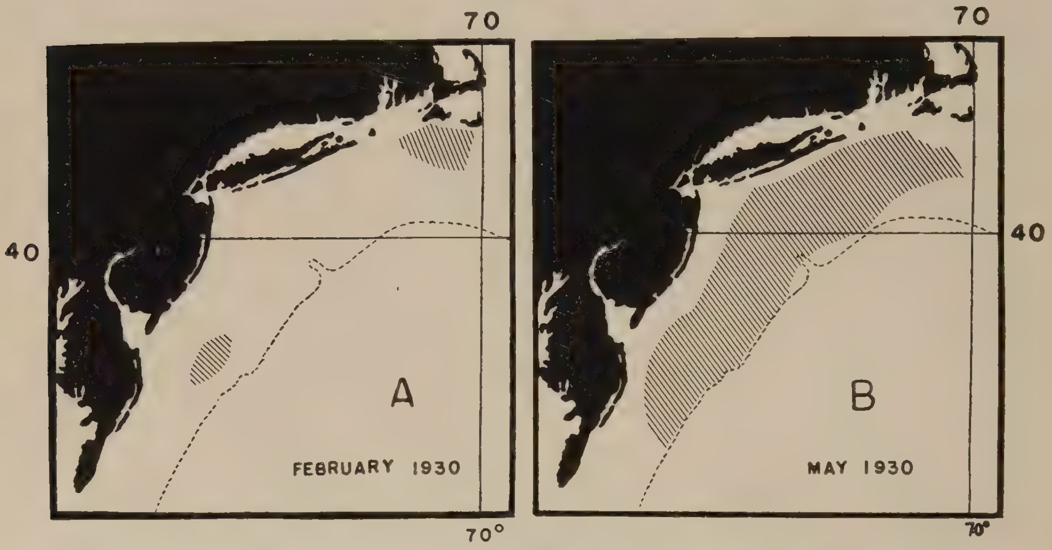


Fig. 12. Areas where *Limacina retroversa* made up more than 10% of the total volume of plankton: A, February 5–13, 1930; B, May 12–23, 1930.

The general result of these mutual fluctuations among the leading species is, that while the percentage of Calanus, for the area as a whole, has averaged about the same in May as a month earlier, its rank, relative to its nearest competitors has averaged lower in May than in April, but that of Limacina and of *Sagitta elegans* much higher. Consequently, if we name April the "Calanus" month, we might equally name May the "Calanus-Limacina-*Sagitta elegans*" month for the area as a whole, and for the offshore belt. But the average ranking for May in the inshore belt, and in the southern sector, is the reverse, i.e., "Limacina-Calanus." And the picture is not greatly altered, even if one very productive catch of Limacina (2666 c.c., midway out on the Corson profile, May 20, 1930) be omitted from the calculation.

Apart from fluctuations in the relative strengths of the leading species as just outlined, the most interesting alteration from April to May is increasing diversification in the general community made evident by the fact that the list, for the latter month, of other species that have averaged as much as 1% (Table, p. 229) includes larval euphausiids, and crab larvae (these had already appeared in significant proportions, locally in April), besides *Oikopleura labradoriensis*, *Aglantha digitale,* leptoline medusae, and salps. Analysis of the rich (> 500 c.c.) hauls points in the same direction, for while the eight leading species were responsible for 80%, or more of the catch in every rich haul in April, this was the case in 38, only, out of 46 such cases in May. We may also note that *Calanus hyperboreus* (which did not form as much as 1% of any April catch) constituted 2–11% of the 14 rich catches that were made in May, in 1930, occasionally also in 1932. However, the list of species, which—while never averaging 1% for any cruise as a whole—have reached that level at individual stations, is shorter for May than for April, as follows:

> *Acartia longiremis,* 4 stations, 5–16 c.c., 1–7%; amphipods, 2 stations, 4 and 23 c.c., 2 and 4%; anthomedusae, 1 station, 85 c.c., 36%; Arachnactis larvae, 1 station, 16 c.c., 9%; *Candacia armata,* 3 stations, 8–38 c.c., 3–22%; *Centropages hamatus,* 7 stations, 5–59 c.c., 2–26%; *Clione limacina,* 10 stations, 3–75 c.c., 1–13%; Doliolum sp., 2 stations, 53–80 c.c., 8–61%; *Euchirella rostrata,* 1 station, 3 c.c., 1%; Evadne sp., 1 station, 9 c.c., 2%; *Mnemiopsis leidyi,* 1 station, 8000± c.c., 90%; mysids, 1 station, 2 c.c., 1%; *Oikopleura dioica,* 1 station, 7 c.c., 7%; *Paracalanus parvus,* 1 station, 14 c.c., 7%; *Paraeuchaeta norvegica,* 1 station, 27 c.c., 15%; *Pleuromamma gracilis,* 5 stations, 6–18 c.c., 1–10%; *Rhincalanus nasutus,* 9 stations, 4–74 c.c., 2–24%; *Temora longicornis,* 1 station, 10 c.c., 4%; *Temora stylifera,* 1 station, 2 c.c., 4%; Tomopteris sp., 1 station, 2 c.c., 5%.

And the only rich centers for any member of this list in May was a swarm of lobate ctenophores off Currituck, on May 15, 1929 (p. 371).

It is especially interesting that the percentage of benthonic derivatives, of all sorts, combined, i.e., decapod larvae, gammarids, mysids, and leptoline medusae, was so low in May for the area as a whole (maximum, 8%, May 1931), even in the inshore belt, where the depth of water is less than 50 meters for most of the area included. The relative paucity of oceanic forms of any sort anywhere in May is also worth emphasis, for salps, representing this group, assume some importance locally later in the season (p. 240).

June. The percentages for the eight leading species have averaged about the same for June (72–97%, Table, p. 229), as for May (63–92%), and the list of dominant species includes only one member (Clione) on any June cruise, that does not appear in the list for May. Calanus, on the whole stands relatively somewhat higher in June than in May, ranking first, by far, in three of the years (1929, 1930, 1931) and about equalling its closest rival (Aglantha) in the fourth year (1932), whereas in May, it ranked second in two of the four years, first in two only. And a still more definite trend in relative importance, upward from May to June, appears, for Calanus, in the relative frequency with which it has formed upwards of 80% in the rich (> 500 c.c.) catches, for this happened in 3 out of

18 such cases in April, in 4 out of 40 cases in May, and in 17 out of 36 cases in June, but not at all in February. On the other hand, it appears that no significant alteration is to be expected from April through June, in the inshore-offshore and north-south gradients for *C. finmarchicus*, for it has averaged in about twice as great percentage offshore and in the north, as inshore and in the south, throughout this part of the year (Table, p. 229). And this last generalization is further supported by the fact that very strong dominance by Calanus (80%) is also much more frequent offshore in June (25% of the stations) than inshore (7% of the stations), whereas relative scarcity (less than 5%) was much less frequent offshore (12% of the stations) than inshore (26% of the stations).

Lest the reader gather the impression from the foregoing that Calanus (or any other species for that matter) is distributed with anything approaching relative uniformity over our area, at any season, we must, however, emphasize the fact that this is very far from the truth. Actually, a chart for any given cruise, whether for relative abundance, or for absolute, shows wide and irregular variations within short distances.

Sagitta elegans also increased appreciably in relative importance from May to June in three of the years (1929, 1930, 1932), in fact, doubled in one (1932), its trend being also upward, in the rich (> 500 c.c.) hauls, though this increase was not sufficient to bring it into rivalry with Calanus. In the fourth year (1931), it showed no definite trend in percentage, one way or the other, during this period. It has also averaged much more important inshore (about 27%, for all years combined) than offshore (about 7%), in June, just as in May but with no consistent contrast between north and south.

Limacina, contrasting with *C. finmarchicus* and *S. elegans*, decreased in importance from May to June, in each year, its average percentage for all cruises combined being only 1/3 as great in the latter month (8%) as in the former (20%) in the north, only 1/5 as great in June (5%) as in May (26%) in the south. Similarly, it formed 80% of the total catch in only one of 39 rich (> 500 c.c.) hauls in June, contrasting with 5 out of 41 such cases in May. It is thus evident that this pteropod has passed its peak in importance by the end of the spring, with a subsequent decline by about 2/3, in its percentage in the plankton, through June, as a reasonable expectation. As a result of this seasonal decline, Limacina, ranking first or second in May has only once ranked second in June (1930), and only fourth or fifth in the other years.

It is doubtful whether any very pronounced seasonal trend in relative percentage in either direction is characteristic for any of the other leading species from May to June. Thus, the percentage of Aglantha, which increased about 4-fold during this period in one year (1932), did not appreciably alter in any other year. The average percentage of Metridia, also, altered very little from the one month to the other in any year, ranging for the whole series only between 1–2% and 6%, though its percentage in the rich catches markedly declined in one year (1930). The period, May-June, also, appears one of relative constancy for the average percentage of Centropages, which did not alter then by more than 1–3% or so, in any year of the series. It is, in fact, during the period, May-June, that this copepod is least important, for it has then averaged only about 1–11% of the total plankton, for the area as a whole, or 1–14% in the inshore belt, contrasted with 1–49% in February. We may also point out that while Centropages monopolized (formed more than 80%) one out of 11 rich catches in February, this was not recorded at all in May and June. And euphausiids, as a group, have also averaged about the same in June as in May, i.e., 1–5%, whether for the area as a whole, or for rich (> 500 c.c.) catches.

Species, however, that rank low in average percentage, may rank high locally, or even dominate, in June, as at other seasons. Euthemisto, for example, which has averaged only 7%, in general, in that month constituted 19–84% in eight out of 48 catches in the year 1930, which ranks it among the leaders, at times. *Clione limacina* also formed 7–73% in 10 June catches in 1932 (bringing its average for that month as a whole up to 5% for the area as a whole), though it did not form as much as 7% at any station in June of the other years, and agalmids ranked high (about 42%) in one June haul of 220 c.c., *Centropages hamatus* formed 26% of another of 218 c.c., (both in 1932) while euphausiids made up 9% of one of the three rich catches (> 500 c.c.) that were recorded for June 1932. These rich spots may perhaps have been potential reservoirs for future local swarms of these species. And it is possible that the following instances where some particular species formed 1% or more of the June catch (listed below) may also be so considered:

Acartia longiremis, 6 stations, 2–15 c.c., 1–7%; *Aequorea aequorea*, 1 station, 11 c.c., 11%; *Agalma okeni*, 1 station, 13 c.c., 1%; agalmids, 4 stations, 4–94 c.c., 3–42%; amphipods, 6–35 c.c., 1–48%; Arachnactis larvae, 3 stations, 8–37 c.c., 1–17%; *Calanus hyperboreus*, 5 stations, 4–17 c.c., 1–6%; *Candacia armata*, 1 station, 6 c.c., 1%; *Centropages hamatus*, 6 stations, 2–189 c.c., 1–60%; Crago sp., 3 stations, 5–35 c.c., 3–13%; cumaceans, 1 station, 2 c.c., 2%; diphyid eudoxids, 1 station, 25 c.c., 4%; Doliolum sp., 3 stations, 19–82 c.c., 3–50%; Eucalanus sp., 16 c.c., 4%; Evadne sp., 7 stations, 2–25 c.c., 1–17%; *Lensia conoidea*, 2 stations, 6–13 c.c., 2–3%; *Mecynocera clausi*, 1 station, 4 c.c., 1%; *Neomysis americana*, 2 stations, 22–100 c.c., 9–83%; *Oikopleura dioica*, 4 stations, 7–17 c.c., 2–17%; *Pleuromamma gracilis*, 1 station, 4 c.c., 3%; *Sagitta enflata*, 2 stations, 2 c.c., 1%; *Temora longicornis*, 6 stations, 2–12 c.c., 2–11%; *Tomopteris catharina*, 1 station, 4 c.c., 4%.

It is especially interesting that benthonic animals of all sorts combined, have averaged no more important in June than in May, for the area as a whole (Table, p. 229), because they may then be the leading forms close in to the land, at localities where the more generally dominant species happen to be only in small amount. Cases in point are *Neomysis americana* (100 c.c.) and crab larvae (68 c.c.) forming 83% and 48% respectively of the total catches, at two stations near the mouth of Delaware Bay in June 1930; crab larvae (70 c.c. and 65 c.c.) forming 19% and 15% near Seagirt and Winterquarter, on two occasions in 1931; and leptoline medusae (120 c.c.) forming about half the catch midway out on the shelf off Martha's Vineyard on June 19, 1932; this last instance being particularly interesting because the source of supply in this case was probably Nantucket Shoals, i.e. to the eastward. On the other hand, salps of one species or another have appeared locally near the outer edge of the shelf in considerable aggregations in June, foreshadowing the much greater importance they assume a month later in the summer (p. 242). They may indeed constitute as much as 9% of the general June average for this belt as a whole, in some years (e.g., 1929, 1932), though in others, as in 1930 and 1931, they may not average more than 1% there, in that month. And in 1929 Doliolum (recorded at one May station, p. 270) had entered the southernmost sector in such numbers by June, that it was not only omnipresent then along the Hog Island and Chesapeake profiles, but constituted 21% of the average catch there, though not detected at all at any of the stations farther north, or anywhere within the confines of our area in any other June, for that matter. But the increase in the relative abundance of salps and Doliolum has not been accompanied by any corresponding increases in the number of oceanic species encountered. On the contrary, fewer of these species were detected in June than in May.

The combined annual tabulation for June (p. 267)—probably representing the normal ranking for the month better than the percentage distribution for any one individual cruise—shows Calanus so far in the lead offshore and in the north, that it outranks its closest competitor (*Sagitta elegans*) more than 2 to 1 for the area as a whole. *S. elegans* about equals Calanus inshore, however, and in the south. The lower rankings for June have shown wide variation from year to year, second for the region as a whole being either *S. elegans*, Limacina, or Aglantha, third, *S. elegans*, *Centropages typicus*, or Pseudocalanus, and fourth, *S. elegans*, *Centropages typicus*, Metridia, Limacina, Euthemisto, or euphausiids.

July. The data for July are confined to one general cruise in 1929, and two in the northern sector (north from Barnegat) in 1930 and 1931. But the results of these, added to previous information for the summers of 1913 and 1916 (Bigelow, 1915; 1922) give, at least, an indication of the seasonal succession, and of the orders of magnitude to be expected in normal years.

If we omit, from our calculations, one phenomenally rich catch of salps (67109 c.c.), at the edge of the continent off Cape May, July 18, 1929, the relative volumetric strengths of the leading species in the July catches have averaged as tabulated on page 229. In the year 1929, which may perhaps be accepted as representing the median condition, the most striking alterations from June to July, for the region as a whole (Fig. 11), were (A) that *Sagitta elegans* had forged ahead of Calanus throughout the inshore belt, though still lagging behind it offshore, (B) that *Centropages typicus*, which had fallen to a low rank by May and June (p. 229) had again tripled in relative importance by July, i.e., was then about 1/2–2/3 as abundant, volumetrically, as Calanus in the north (indifferently offshore-inshore) and ranked ahead of Calanus to the south.

Euthemisto compressa should perhaps be ranked higher in relative importance for July than might be suggested by its low percentage (1–6%) for the several years combined, because local centers of high abundance may develop for it. In 1929, for example, it formed 28% of a rather small catch (67 c.c.) on one occasion (St. 20556) near Cape May; in 1930, again, it formed 35% of the total at a station near Shinnecock, and it was found swarming midway out on the shelf off Martha's Vineyard and off Montauk in July 1913 (Bigelow, 1915, p. 281). The case is parallel for *Temora longicornis*, for while this copepod did not average as much as 1% on any July cruise, it formed 1–2% of the rich (> 500 c.c.) catches on three occasions in 1931, while in 1916, it swarmed near Martha's Vineyard (Bigelow, 1922, p. 146). *Clione limacina*, may, likewise, be relatively prominent locally in July, for it formed 9% of a 540 c.c. catch close in to New York on one occasion in 1930, though it did not average as much as 1% on any July cruise as a whole. It is also suggestive, on the negative side, that while euphausiid larvae formed 35% of one rich (> 500 c.c.) catch, offshore, off New York, in July 1929, euphausiids as a whole altered but little in importance from June to July, their respective percentages being < 1% inshore and 6% offshore for the former month, < 1% inshore and 6% offshore for the latter, in the year in question. And leptomedusae, which (in 1929) had formed 2–11% of the catch, at a few stations in the northeasternmost sector in June (p. 240), had practically vanished thence by the following month.

On the other hand, the siphonophores (*Muggiaea kochii, Lensia conoidea,* and unidentifiable agalmid fragments) may locally constitute as much as 8–10% midway out on the shelf in the southernmost sector as, for example, in 1929 off Chesapeake Bay and off Winterquarter. Ctenophores (*Pleurobrachia pileus* and *Mnemiopsis leidyi*), also may become the dominant group inshore and to the south in midsummer, even practically monopolizing the water there at that season in some years, e.g., 1913, as described below (p. 369, 370), though they are insignificant in importance in other summers, as in 1929, when only one rich center was recorded for them. And it appears that the case is similar for at least one category of visitors from offshore, namely, the salps, which were dominant close to New York and locally elsewhere well inshore by the first of August in the summer of 1913,[1] though curiously enough, they only occurred sparsely farther out on the shelf at the time (Bigelow, 1915, p. 270). But seemingly it is only in exceptionally warm years that this occurs, for while salps formed 24% of the average catch offshore in July 1931, and swarmed locally near the 200-meter line in that month of 1929, they were recorded only occasionally inshore at that season, in 1930 or in 1931, and not at all on the shelf in the cold summer of 1916, though locally abundant out beyond the continental edge at the time (Bigelow, 1922, p. 156).

The scarcity of salps inshore, in most summers, added to the facts that *Rhincalanus nasutus* showed no increase in relative importance from June to July in 1929, 1930, or 1931, although generally distributed in the latter month, that Doliolum did not increase relatively from June to July in 1929 (the only year when recorded at all inside the 200-meter line), and that other oceanic forms have been negligible volumetrically, in on the shelf, in all the summers of record is sufficient evidence that mass invasions of the northern part of our area by visitors from warmer waters offshore, are exceptional events, even at the warmest time of year. In fact the only "tropicals" ever likely to be of volumetric import there, are such as are capable of very rapid multiplication—e.g., salps. Contributions rom mid-depths along the slope, of the category represented by *Eukrohnia hamata* and *Paraeuchaeta norvegica* have also been insignificant inside the 200-meter curve, north of Delaware Bay, in every year of record (p. 250), at all seasons.

In normal years, in short, the waters in the northern sector are as strongly dominated in July as in June by the boreal assemblage, lead by Calanus, Centropages, and *Sagitta elegans*, whether judged by the fact that these three species together have averaged about 86% in all July hauls combined in that sector, or by their prominence in the rich (> 500 c.c.) centers, of which they have on the average constituted about this same percentage for the several years combined, in that month. In the southernmost sector, however, represented by the Winterquarter, Hog Island, and Chesapeake Bay profiles, a considerable invasion by warm water species was indicated in 1929, by the presence, in July, of 3% (on the average) of the southern appendicularian, *Oikopleura dioica*, 5% of *Muggiaea kochii*, 10% of Doliolum, 3% of *Lucifer typus*, 3% of the phyllosome larvae of Palinuridae, and 9% of sundry oceanic copepods in combination. And the occurrence of phyllosome larvae there is especially interesting as evidence of the infiltration of a neritic species from far to the southward, no doubt by the offshore route, because the northern boundary for their probable parent, the spiny lobster (Panulirus) is Cape Lookout in North Carolina in Latitude about 35° N.

---

[1] No precise quantitative data available for that year.

Yet, even with this invasion of oceanic forms, the list of species, which, while not equaling 1% in any subdivision of the area on any July cruise, hence not discussed above, have formed 1% or more at particular stations, is considerably less extensive for July than for June or May, as follows:

> *Acartia longiremis*, 2 stations, 4–9 c.c., 1–3%; agalmids, 1 station, 9 c.c., 8%; *Calanus hyperboreus*, 1 station, 6 c.c., 1%; *Candacia armata*, 6 stations, 3–22 c.c., 2–17%; *Eucalanus attenuatus*, 2 stations, 4–89 c.c., 4–36%; Evadne sp., 1 station, 4 c.c., 1%; Phronima sp., 1 station, 13 c.c., 1%; Podon sp., 1 station, 6 c.c., 7%; stomatopod larvae, 1 station, 4 c.c., 1%; *Temora longicornis*, 4 stations, 2–26 c.c., 1–2%; *Temora stylifera*, 1 station, 26 c.c., 9%.

Autumn. Quantitative information is lacking for August and September. But, if October data for the one year of record (1931) be representative, as seems probable, it appears that early autumn sees a notable decrease in the relative importance of Calanus, the percentage of which declined in the offshore belt[1] in that year from 61% in July to 8% in October in the northern sector, and from 41% in June[2] to 7% in October in the southern. In fact, the maximum percentage of Calanus in any of the richer (> 300 c.c.) October hauls, was only 16%, contrasted with frequent percentages of 80% or more in summer and spring, while there was one October haul without Calanus. The average percentage of salps also decreased in the northern sector, offshore, from 24% in July to less than 1% in October, though *Iasis zonaria* then formed 51% of the total catch of 112 c.c. at one station off Winterquarter in the south. On the other hand, *Centropages*

---

[1] The October cruise of 1931 was confined to the offshore belt.

[2] The July cruise was confined to the northern sector.

typicus, which had been negligible in June and July of the year in question, so greatly increased relatively (as well as absolutely) during late summer, or early autumn, that by October, it ranked far above its closest rival (Paracalanus) in the north (47%) and slightly so, in the south (14%). Perhaps even more striking in that year was the autumnal increase in the percentage of Paracalanus, which did not average more than 1% in any considerable subdivision of the area in any summer of record, but which formed 26% offshore in the north, and 12% in the south, in the October in question. *Metridia lucens*, also, increased in the north from 1% to 11% between July and October, but was in about the same percentage in the south in the latter month (2%) as it had been in June (1%). Other species showing smaller, or less regular increases from June or July to October are Pseudocalanus from less than 1% (June) to 4% (October) in the south, but with little change in the north; *Sagitta serratodentata*, from less than 1% in June to 2% in October in the north and from 2% in June to 9% in October in the south; while *Sagitta enflata*, *Oikopleura dioica*, and Penilia, which did not enter into the picture at all in the north in July or in the south in June, averaged 6%, 2%, and 8%, respectively, of the catch in the latter sector in October. However, none of the other members of the community that constituted as much as 1% of the average catch for that October had experienced any significant change in relative importance since June (in the south) or July (in the north). And the list of species forming 1% or more at individual stations had not lengthened appreciably in this same period:

Acartia sp., 2 stations, 1–4 c.c., 4–6%; agalmid, 1 station, 9 c.c., 4%; *Candacia armata*, 2 stations, 3–14 c.c., 3–11%; *Centropages violaceous*, 1 station, 1 c.c., 1%; Corycaeus sp., 1 station, 3 c.c., 3%; *Mecynocera clausi*, 4 stations, 1–4 c.c., 1–4%; Oncaea sp., 1 station, 9 c.c., 11%; *Pleuromamma gracilis*, 1 station, 2 c.c., 1%; *Scolecithrix danae*, 2 stations, 3–14 c.c., 2–12%; *Temora longicornis*, 1 station, 1 c.c., 1%; *Temora stylifera*, 2 stations, 1 c.c., 1%.

These mutual changes in relative abundance result in a reversal in relative ranking, from summer (Table p. 267) to mid-autumn, when Calanus ranked only fourth instead of first, but Centropages first instead of third, fourth, or fifth (Fig. 11), with second place falling to Paracalanus, the highest ranking of which was not above fifth on any July cruise, while it does not appear at all in the lists of dominant species for April, May, or June.

No data as to the relative abundance of the various species are available, for the three month period, November to January, of any year.

Annual Differences

It was a fortunate chance that so short an observational series should have included one year (1932) when the late winter was unusually warm in the waters of our area, one (1913) in which the summer was warmer than normal, and one (1916) in which it was colder, making it likely that such annual variations as were recorded cover the range commonly to be expected from year to year.

It is not astonishing that typically boreal species such as *Calanus finmarchicus* and *Sagitta elegans* were relatively less prominent at the end of a winter of the type represented by 1932 than in the other years. And the high percentage of Paracalanus in that same February may also have been associated with temperature. But temperature offers no apparent explanation for the facts that one of the two years when *Centropages typicus* ranked high (1930) is to be classed as cool, the other (1932) as warm; or that while *S. elegans* was the dominant form in one of the cool winters (1931), it was of only very minor importance in the other (1930). And we can merely note that annual variations in the relative ranking of the several dominant species were much wider in the offshore belt than inshore. No doubt the explanation for this lies in the fluctuations of conflicting water masses along the edge of the continent.

Following an abnormally warm winter (to judge from 1932), Calanus continues much less important relatively than usual, as well as less abundant, through May and June, even though the temperature anomaly may have entirely disappeared by mid-spring. On the other hand, Aglantha, Limacina, and *Sagitta elegans* ranked much higher in that June than in any other. The chief variation from year to year later on in the summer—and one of considerable significance from the standpoint of the fertility of our region as a pasture for plankton-eating fishes—is that Calanus and its companion species dominate much farther southward in cool and average summers, than in what may be classed as "warm," at least along the outer part of the shelf. On the other hand, ctenophores (Mnemiopsis and Pleurobrachia), combined with salps, play a dominating rôle to the southward, especially inshore, at least in some warm summers, but are not volumetrically significant over any extensive areas in cool. The one extreme in these respects may be illustrated by 1929, when *Calanus finmarchicus*, *Centropages typicus*, and *Sagitta elegans* formed even a larger percentage of the total catches for the southern sector as a whole in July (average, 58%) than they had in June (34%) or in May (27%),[1] except at one station close to the 200-meter contour off Cape May, where salps swarmed (p. 241). And Calanus was also the leading species, offshore, southward of New York in the summer of 1916—likewise a cold year—along a narrowing belt to the offing of Chesapeake Bay as described elsewhere (Bigelow, 1922, p. 139). The opposite extreme was illustrated by the summer of 1913, when copepods, which were in rich aggregations over the continental shelf south of Cape Cod, were "counted by individuals" south of New York (Bigelow, 1915, p. 285), instead of by hundreds of cubic centimeters, while in some of the southern hauls no copepods at all were detected. *Sagitta elegans* was, also, so scarce south of New York in that summer that none of the 19 subsurface hauls yielded more than odd specimens of it there, which applies equally to Limacina, to Euthemisto, and to euphausiids as a group.

---

[1] 93% in April, 34% in May, 50% in June, and 64% in July.

It is an interesting question whether it is characteristic of warm summers that the poverty of the Calanus community, from New York southward, is compensated for—especially in the inshore belt—by swarms of ctenophores (Mnemiopsis and Pleurobrachia) and of salps, as happened in 1913 (Bigelow, 1915, p. 270). Unfortunately, no data are available for July for 1932, the year of the present series that seems the most pertinent in this connection. But the fact that ctenophores were found swarming locally in May (p. 237), in June (p. 369), and in July (p. 242), combined with widespread presence of salps in the offshore belt at that season, and occasionally in abundance (p. 242), makes it likely that our area is always sufficiently seeded with members of these groups throughout the vernal half year, for rapid multiplication to take place when circumstances favor.

No information is available as to annual variations in the relative abundance of different species for autumn or early winter.

Sources of the Local Plankton

The planktonic community of our area, like that of the Gulf of Maine, consists in great majority of holoplanktonic species. The only benthonic derivatives that have averaged as much as 1% of the total volume in either subdivision of the area at any season, have been small leptoline medusae, which may form up to 4% for the area as a whole in May (Table, p. 229), and the larvae of crabs or of hermit crabs, which may swarm locally next the land in July (p. 286), and form up to 1–5% offshore as well, in late spring and early summer in some years (Table, p. 229). Perhaps we should also so classify (because of winter eggs) the cladoceran, *Penilia schmackeri*, which formed 8% offshore in the south in the one October of record.

Indigenous species also greatly predominate, in volume, over immigrant, at all seasons, having (on the average) formed upwards of 92% of the total volume of plankton for the area as a whole in February, 95% in April and May, 89% in June, 84% in July (of the one year when the entire area was surveyed) and 89% on the one October cruise. Immigrant species were in fact negligible in February and April, except for salps which may appear in small percentage in the offshore belt, even this early in the year (p. 272). With the advance of the season, other immigrants enter, however, in small amount into the "dominant" list (> 1%), some from the colder waters from the east, others from the continental slope offshore. The members of the first of these categories, represented in May and June by *Oikopleura labradoriensis*, by *Calanus hyperboreus*, and perhaps by the lobate ctenophore Bolinopsis, have never in our experience been of any volumetric importance even in the easternmost sector which is most open to their entry. And except for salps, visitors from offshore are equally insignificant in the volumetric total in the northern sector, even offshore, in spring. But they play a somewhat more important rôle by midsummer in the southern sector, where, in 1929, tropical decapods and copepods, Doliolum, salps, and siphonophores together formed about 15% of the average catch. And the state is similar in autumn, judging from the fact that in October 1931, offshore chaetognaths and oceanic copepods, in combination, formed 18% in the offshore belt in the south.

The lists also include a considerable variety of other immigrants, besides those just mentioned, which—if never plentiful enough to be of any volumetric importance within our limits—promise to be of such value as indicator-species that they deserve some discussion from that viewpoint, even though this be somewhat foreign to the main thesis of the present report. Indicator-species, from whatever source, may be grouped for convenience into two categories. The one group comprises those species that either fail to breed in exotic surroundings, so that their presence there endures only for the span of life of the entrant individuals, or which—if they do succeed in breeding—vanish shortly after the immediate effects of active invasion by exotic waters have ceased. The localities of occurrence of the members of this group yield direct evidence as to short term intrusions of waters of one or other origin into our area. The second category comprises the considerable variety of species that, while regularly indigenous, vary periodically in abundance as water of one or another origin is in the ascendency. In the long run, it is from this group that we may expect the more reliable information as to the secular variation in the proportionate amounts in which the different waters mingle. For an excellent example of this we may refer to the information that the mutual fluctuations in abundance of *Sagitta elegans* and *Sagitta setosa* have yielded as to variations in the proportionate amounts of Atlantic and of Coastal waters in the English Channel (Russell, 1935; Kemp, 1938; Furnestin, 1938) and of oceanic and "Bank" water off the east coast of England (Wimpenny, 1937). But trustworthy inferences in this regard must await much more detailed knowledge of the ecological relationships of the animals concerned, than our studies can yet provide.

In the particular part of the sea with which we are concerned, the waters that mingle over the shelf, to maintain the comparatively stable state (as regards temperature and salinity) that exists there, draw chiefly from land drainage on the one side, from the highly saline band along the continental slope on the other, and from intrusions past Cape Cod, of shelf water from the east, which come chiefly in the spring. The planktonic animals that these waters bring with them are subject to a similar classification. But it is doubtful whether any considerable volume of water of shelf origin enters our area past Cape Hatteras from the south, for no direct evidence of this has been detected in the distribution of temperature or of salinity (Parr, 1933; Bigelow, 1933; Bigelow and Sears, 1935).

Within our limits—even in the most southern sector—immigrants from shelf waters further south have been negligible, as was to be expected from the insignificance of water increments from this source that might convey them. In fact, the only species, palinurid larvae, certainly belonging to this category that has been detected in such examination of the catches as has yet been made, may actually enter our boundaries *via* the offshore route, i.e., from the continental edge, for these phyllosome larvae are notoriously subject to extensive northerly drifts along the American slope. Immigrants of the opposite category, namely from more easterly shelf waters, play a much more important rôle, due to the considerable amounts of water from that source, that may enter the eastern sector in the spring in some years, and perhaps to some extent every year. *Calanus hyperboreus* is especially interesting in this respect, its existence being so brief in our area that the fluctuations in its local status very closely follow the waxing and waning of the drifts that bring it past the offing of Cape Cod. *Oikopleura labradoriensis* appears to be slightly more successful as a colonist, for it may breed to some extent, as it drifts westward and southward. But its annual presence within our limits is sufficiently brief for it, too, to serve as a reliable indicator of a more boreal source. So, too, for *Thysanoessa longicaudata* and perhaps for Erythrops. The incidence of the species belonging to this category may indeed prove more reliable as drift-indicators in this particular case, than is the distribution of temperature, because the latter is so nearly alike on the two sides of Cape Cod at the critical season, that it is not easy to follow east-west movements of water there, by their thermal effects.

We can already say that the combined records for these species show the effects of such indrafts as extending widespread over the shelf down at least to latitude 38°, and occasionally to 36°, in one year or another in the months of April, May and June, but that they give no evidence of any significant increment from this source in the later summer, in autumn, or at the end of winter.

Comparison with the plankton of the Gulf of Maine brings out the interesting difference that none of the hauls in our area have yielded so much as a single specimen of the typically subarctic forms, *Ptychogena lactea, Mertensia ovum, Limacina helicina,* or *Oikopleura vanhöffeni.* Neither has *Metridia longa* ever been detected west of Cape Cod, although it occupies much the same faunal niche in the Gulf of Maine to the east that *Oikopleura labradoriensis* does in our area, becoming widely distributed there, and perhaps succeeding in breeding to some extent, in years when it passes Cape Sable in greatest number (Bigelow, 1926, p. 61). The offing of Cape Cod thus appears to mark as definite a transition-zone (probably thermal) for some of the northern planktonic animals as it does for many benthonic forms. Another interesting regional contrast is that while our area and the Gulf of Maine both receive immigrants from the east, these tend to disperse much more generally over the shelf west and south from Cape Cod, than is the case in the Gulf, where the shorter-lived, subarctic immigrants have been most frequently encountered either in the eastern side or—if further west—within about 30 miles or so of the land; in other words in the track of the peripheral anticyclonic drift (Bigelow, 1926, p. 59; Fish and Johnson, 1937, p. 248).

Little can be said as to the magnitude of the contribution that waters coming from the east—i.e., from George's Bank or the Gulf of Maine—makes to the volume of plankton in our area, because much the same assemblage of species usually dominates the community to the east as well as to the west of Cape Cod; the few that are sure indicators, within our limits, of this eastern source are relatively unimportant in the Gulf also, so far as volume is concerned.

The basin of the Gulf of Maine, at depths greater than about 150 meters might be described—without much exaggeration—as a lateral extension of the slope water habitat *via* the Eastern Channel, so far as temperature and salinity are concerned. And this is reflected in the fact that its deeper strata constantly support a considerable endemic population of the boreal mid-water copepod, *Paraeuchaeta norvegica,* and of the decapod genus, Pasiphaea, with a sparse but generally distributed immigrant population of *Eukrohnia hamata.* A scattering of *Dimophyes arctica* of similar origin also occurs there, while *Sagitta maxima* and *S. lyra,* (perhaps the most useful animal indicators of water entering the Gulf of Maine at lower levels) have been taken repeatedly in the deep hauls in the basin. No topographic parallel to this particular situation exists west or south of Cape Cod, for while the submarine gorge off the Hudson River, and the others farther south that have recently been mapped by the U. S. Coast and Geodetic Survey (Rudé, 1938) furrow the edge of the continent to a depth much greater than that of the basin of the Gulf of Maine, the extent of area occupied by their troughs is so small that movements of water up their slopes would not be expected to contribute much to the communities existing over the neighboring shelf. On the other hand, the whole frontage of the latter is open to direct influences of this sort from the continental slope.

Actually, *Paraeuchaeta norvegica, Sagitta maxima,* and *Eukrohnia hamata* complete the list of immigrants from offshore that are reliable indicators of water from the deeper levels within our area, for we have no record at all of *S. lyra* or of *Demophyes arctica* within our limits, nor did the towings for the period, 1929–1932, yield a single representative of the bathypelagic community of black fishes that Beebe (1929) found so abundant in the mouth of the Hudson Gorge, of red prawns, or of deep water medusae. The very paucity, however, of what we may name the "Paraeuchaeta" community makes them (when they do occur on the shelf), the more reliable indicators of highly saline water, expanding shoreward up the bottom slope. By this evidence, water movements of this sort have no significant effect as agents of mass transport beyond the 100-meter contour.

Monthly ratios of records of Paraeuchaeta, Eukrohnia, and *S. maxima* combined, to total number of offshore stations, of 1.1 to 1 for February (32 records); 0.6 to 1 for May (55 records), 0.1 to 1 for June (8 records), and 0.1 to 1 for July (4 records), with no records at all for October, point to such indrafts as decreasing somewhat either in frequency or in volume from late winter through spring to summer, seemingly to cease entirely in early autumn.

The great majority of the records for this group lie within 20 miles or so of the edge of the continent, though occasionally dispersed farther inshore, as discussed under the individual species concerned. But they are scattered all along this offshore belt, from the one boundary of the area to the other, without apparent concentration in any particular sector.

The records inside the 200-meter contour for species which (while equally surely of offshore origin) may have come in with the upper strata of water, are not only much more numerous (Fig. 13), but this group is qualitatively much more varied for it includes salps and Doliolum; the decapod, *Lucifer typus*; the amphipod, Phronima; the euphausiids, Stylocheiron, Thysanopoda, and Euphausia; the copepods, Eucalanus, Euchirella, Pleuromamma, Rhincalanus, *Centropages violaceus*, *Mecynocera clausi*, Sapphirina, *Scolecithrix danae*, *Calanus minor*, *Undinula vulgaris*; the pteropods, *Corolla calceola*, *Creseis acicula*, *C. conica*,

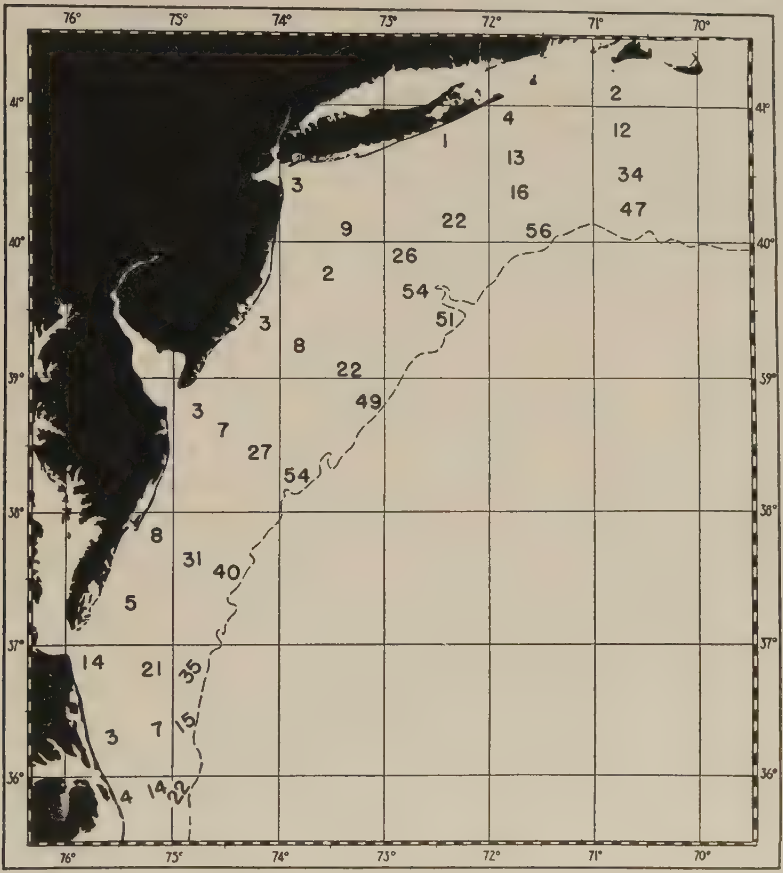


Fig. 13. Numbers of records at different localities, for tropical oceanic species listed on this page.

C. virgula; the heteropod, Firoloida; the chaetognaths, *Sagitta hexaptera*, *Pterosagitta draco*, and *Krohnita subtilis*; the medusae, Niobia and Aglaura (Bigelow, 1915); and the siphonophores, Abylopsis, Bassia, *Agalma okeni*, *Ceratocymba sagittata*, *Eudoxoides spiralis*, *Chelophyes appendiculata*, *Lensia fowleri*, *Vogtia pentacantha*, Physophora, and Physalia. *Candacia armata* and *Sagitta enflata* also depend on immigration, from the continental slope, for their continued existence on the shelf, though perhaps breeding there to some extent locally (pp. 318, 356), while the palinurid larvae may also reach our southern sector via the offshore route (p. 243). The localities of capture, for this group as a whole, have been most numerous at the outermost stations, i.e., within 10–15 miles of the 200-meter contour, progressively less and less so in toward the land (Fig. 14), as distance from their source of origin increases, though occasional members of the group have been taken even close in to the coast here or there as noted elsewhere. The most interesting feature of the distributional chart is, however, that the records for the category as a whole have been about as frequent, relatively, off one sector of the coast as off another (apparent concentrations on the chart result from the geographic locations of the several profiles and the number of stations on each), corresponding to the fact that the slope water with its oceanic fauna, not only fronts the entire length of our area, but lies as close to the 200-meter line in one place as in another, and with successive isotherms tending on the whole to parallel the trend of the continent. In fact, a majority of the species here used as indicators of that source have long been known to occur in this belt much further to the north and east.

The obvious implication is that the mixture of offshore oceanic water with inshore shelf water takes place all along the outer edge of the shelf westward and southward from the offing of Martha's Vineyard past that of Chesapeake Bay. This contrasts with the situation in the Gulf of Maine, where indrafts of this sort enter chiefly in the eastern side, and where records of oceanic indicators have not only been far less numerous than is the case west and south of Cape Cod, but confined for the most part to the peripheral belt, just as are those for arctic indicators (Bigelow, 1926, Fig. 31).

The average number of records for this category of species (omitting *Sagitta enflata* and Candacia which may reproduce to some extent within our limits) was 2.4 per offshore station in February, 2.4 in April, 3.1 in May, 2.6 in June, and 2.7 in July, but 4.6 in October, for the period 1929–1932. This seasonal distribution suggests that immigration is as active in one month as another from the end of winter through spring and summer, but somewhat more so in autumn. In this connection, it is perhaps appropriate to point out that averages of about 3.4 records per offshore station for species of this category for all months combined in 1930, 3.4 record in 1931, and 3.6 record in 1932 do not suggest any wide difference from year to year, during the three year period. And while the average for 1929 was somewhat smaller (about 1.5) it may not have been significantly so, in view of the roughness of the methods employed.

The catches have yielded but few species the production of which is known to be closely confined to the immediate vicinity of the land, and which can consequently be classed as reliable indicators of drifts of water seaward from the coast-line out over the shelf. Among such are the larvae of the blue crab (Callinectes); the mysid, *Neomysis americana*; the copepods, *Acartia clausii* and *A. tonsa*; and the cladoceran genera, Podon and Evadne. Stomatopod and palinurid larvae also fall in this same category, but may more immediately be indicators of offshore water in the particular region in question (p. 243). And the bottom habitats of other benthonic derivatives so far detected in the catches, such as the larvae of other species of crabs, the decapod-shrimp, Crago, and the various leptoline medusae, extend to depths so great that the contribution of their pelagic stages to the plankton of the overlying waters may take place well out on the shelf. We may refer in this connection to the hydroids that have been found floating—and apparently growing—near the surface over George's Bank in spring and summer (Bigelow, 1914, p. 414; 1926, p. 379; Fraser, 1915, p. 306).

In the case of the blue crab larvae, the captures extended 50 miles out, off Chesapeake Bay (Bigelow, 1915, p. 271). Captures of *Acartia clausii* and *A. tonsa* (the latter for 1916 only) were however coastwise (p. 303). Most of the records of Neomysis likewise lie within a few miles of land. In short, the contribution, from this general source, to the planktonic community of the continental shelf, even in the inshore belt—has proved negligible, except locally and temporarily, close in to the land, which parallels the situation in the Gulf of Maine. Neither have we any record out at sea of the scyphomedusan genus Aurellia, anywhere west or south from the Martha's Vineyard profile, though it is plentiful at Woods Hole at the one boundary of our area, and in Chesapeake Bay at the other (Cowles, 1930), or of Dactylometra, which swarms in summer in estuarine situations along our middle Atlantic coast. But since no particular watch was kept for large medusae (as has been done in the Gulf of Maine), the inference to be drawn from their failure in the collections, is only that they were not dispersed seaward, in any summer of record, in sufficient numbers to be picked up in the nets.

On the other hand, the records for Evadne were widespread across the whole breadth of the shelf, with those for Podon also extending well out (p. 346), which suggests considerably wider dispersal offshore for these cladocerans within our limits than in the Gulf of Maine (Bigelow, 1926, p. 307; Fish and Johnson, 1937), where the dominant drift is more definitely peripheral.

THE AREA AS A FEEDING GROUND FOR PLANKTON-EATING FISH

It is common knowledge that the groups of animals ordinarily dominant in the plankton of our area are staple food for fishes in boreal seas generally, and that the particular species of copepods, pteropods, amphipods, and sagittae, with which we are here concerned, are leading items in the diet of the mackerel within our limits (Bigelow and Welsh, 1925, p. 201), as well as in that of the herring in higher latitudes.[1] In fact, the only occasions when any considerable fraction of the animal plankton of our area is not what we may term "nutritive" fish food, are when ctenophores, medusae, or salps may temporarily dominate the local community.

The various analyses that have been published of the chemical composition of planktonic animals show considerable differences in the percentage of proteins, carbohydrates, and fats, not only between different groups and species, but even for the same species at different times and localities. Brandt (1898), Rosenwald (1904), and Delff (1912), for example, long ago showed that the fat content of the dry matter in copepod plankton at different localities in North European waters, may be as high as 12.5% or as low as 5%, while Wimpenny (1929, p. 19) records 9.3%–36% of fat in the dry matter of different samples of plankton dominated by various species of copepods, sagittae, Oikopleura, and other organisms. Especially pertinent in the present connection is Orr's (1934) observation that adult Calanus may have from 10.5–29.6% of fat in the female and 18–33.7% in the male, at a given locality at different seasons.[2] And the presence of about 30% of ether extract in dried Calanus collected off New York in May 1929, as determined by Dr. Th. von Brand at the Woods Hole Oceanographic Institution, even after long preservation in formalin, shows that this copepod may be at least as rich in fat in the western side of the North Atlantic as it is in the eastern. Five per cent of ether extract in the dry matter of Limacina preserved in formalin, similarly, confirms Rosenfeld's (1904) early report of 7.3% fat for this pteropod. So far as we are aware, sagittae have not previously been studied from this point of view, although they enter largely into the dietary of various fishes. But recent analyses by Dr. von Brand of the dry matter of freshly caught *Sagitta elegans* showed about 16% of ether extract (fats plus lipoids). Dr. von Brand also informs us that in samples preserved in formalin (and hence comparable to the plankton volumes with which we are dealing), the dry weight is about 12% of the wet weight in *Calanus finmarchicus*, a value falling well within the range reported by various authors for copepod plankton, and about 11% of the wet weight in Limacina,[3] but only about 7% in *Sagitta elegans*.

---

[1] For a recent study of the relative importance of the different species in the diet of the herring in the North Sea, see Savage, 1937.

[2] For summaries of early analyses, see Steuer, 1910, pp. 656–659.

[3] No doubt the shells of the latter had lost some of their lime in the preservative.

The foregoing suggests that while Calanus in good condition ranks far above most of the other dominant species, if judged by fat content, the other crustaceans may be grouped with Limacina and with *Sagitta elegans*, while the high ratio of wet weight to dry in the latter is perhaps balanced by the high percentage of chitin in crustaceans, and of lime in Limacina. Comparisons of this sort fail, however, to include any estimate of the relative digestibility of these different groups, which no doubt differs for different species of marine fishes, a vital matter as to which we still remain wholly in the dark. Lacking information in this regard, we base the following discussion on the assumption that the crustacean, molluscan, and chaetognath fractions can be justly combined as being of high nutritive value, leaving the salps and the watery ctenophores and medusae out of account altogether, as being of low. Subtraction of the latter does not appreciably affect the picture for February or for April, when medusae, ctenophores, and salps combined, formed less than 1% of the total catch, in each year's record. And these may continue negligible (not more than 1%) right through the later spring and summer, as happened in 1930. But they formed, on the average 9% of the total plankton in May and June, and 10% in July of the other years combined, with a maximum of 22% for the area as a whole in June 1932, percentages large enough to be of some significance in relation to the nutritional value of the general community.

The distributional pictures for the volumes of plankton surface to bottom after omission of the non-nutritive group, would represent what may be termed the potential richness of the area as a feeding ground for fishes. But it is obvious that some levels will be richer than others, some poorer, unless the vertical distribution of the plankton be uniform. Average volumes as calculated for the water column as a whole may therefore be a considerable understatement of actual richness as this affects the fish population. For example, a given locality might well be much richer, at some one level, than might be suggested by an average volume derived from the combination of a poor catch shoal, with a large catch deep, or vice versa. The ratios of the richest catches (irrespective of depth) to the average volumes for the column as a whole, in the months when tows were made at two or more levels, do, in fact, show that such averages considerably minimize the actual richness, at the most productive depth. This is true even at the end of winter when the plankton is most nearly uniform vertically, while in midsummer, the ratio has approached the maximum that is possible for cases where an average has been derived from two values only.

Ratio of volume at level of maximum abundance to average volume for the water column as a whole, for the more nutritive plankton

Month and year	North	South	Inshore	Offshore	General average
Feb. 1932	1.4 to 1	1.4 to 1	1.2 to 1	1.4 to 1	1.35 to 1
Apr. 1929	1.5 to 1	1.6 to 1	1.5 to 1	1.4 to 1	1.5 to 1
May 1929	1.3 to 1	1.7 to 1	1.6 to 1	1.5 to 1	1.38 to 1
1931	1.3 to 1	1.2 to 1	1.4 to 1	1.3 to 1	
1932	1.4 to 1	1.2 to 1	1.2 to 1	1.4 to 1	
June 1929	1.6 to 1	1.4 to 1	1.3 to 1	1.7 to 1	1.5 to 1
1931	1.5 to 1	1.4 to 1	1.5 to 1	1.5 to 1	
1932	1.5 to 1	1.6 to 1	1.6 to 1	1.5 to 1	
July 1929	1.8 to 1	1.7 to 1	1.7 to 1	1.7 to 1	1.8 to 1
1931	1.9 to 1		1.9 to 1	1.74 to 1	

Discussion as to the relative richness of different parts of the area, at different seasons should therefore be based primarily on the volumes existing at the level of greatest abundance. Information in this respect is available for the great majority of the stations of 1929, likewise for most of the offshore stations of 1931 and 1932. But the hauls at many of the inshore stations in the two latter years extended from near the bottom to the surface, hence yielded minimal values only. And these have been adjusted, in the following tabulation, according to the particular ratio that prevailed at the time in the general subdivision in question.

Average volumes at level of maximum abundance, observed or adjusted as above, for the more nutritive plankton

Month	Year	Inshore	Offshore	North	South	Total area surveyed
February	1931	264	153	74	220	199
	1932	660	116	74	519	478
April	1929	304	479	440	324	376
May	1929	265	441	439	178	329
	1931	522	801	640	481	608
	1932	299	497	371	365	361
June	1929	232	447	379	26	312
	1931	784	1124	981	809	908
	1932	251	431	264	410	301
July	1929	480	347	730	313	415
	1931	1294	1178	1322	—	—

If the ratio averaged about the same in 1930 (when only one haul was made at each station), as it did in the other years combined, the volume of nutritive plankton at the level of maximum abundance may be assumed to have been about as follows, in that year:

Month	Inshore	Offshore	North	South	Area surveyed
February	299	59	144	193	187
April	362	451	594	390	279
May	607	1436	896	970	928
June	645	467	630	363	512
July	1080	580	787	—	—

At the end of the winter, according to these tabulations, the amount of nutritive plankton averages smallest in the north and along the offshore belt, where, in fact, the supply may be so poor (less than 75 c.c.) as to make it doubtful whether any considerable population of plankton-eating fishes could subsist, if actively feeding. And while volumes have averaged somewhat larger in the south near shore, the only winter (1932) when even that subdivision could be classed as "rich" (more than 400 c.c.) was one when the water was abnormally warm.

In every year, the volume of nutritive plankton considerably increased in the northern sector by April (1929) or by May, at latest. This vernal augmentation on a broad scale involved the area as a whole, in one year (1931), but it was confined to the northern sector in each of the other two years with average volumes decreasing somewhat in the southern sector in each of these cases from February or April to June or July, resulting in a roughly stationary or slightly downward trend for the area as a whole (Table, p. 229). It follows, in most years, that when volumes reach their peak in the northern sector, which may be as early as May (1930) or not until July (1929, 1931), they average considerably larger there than they do in the southern sector at any time of year, a regional contrast illustrated graphically by the concentration of very large (> 1000 c.c.) catches north of the Cape May profile, irrespective of the season (Fig. 15B). And while the center of summer abundance may, on the contrary, lie in the south after an abnormally warm winter, (e.g., 1932) when large amounts of nutritive plankton exist there in February, the combined evidence of the series as a whole is that the richest pasture for fishes usually develops somewhere within the area outlined in Figure 15; and in July, by which month the average volume of nutritive plankton at the levels of greatest abundance had risen there to about 1300 c.c. in 1931, to about 800 c.c. in 1930, and to about 700 c.c. in 1929, with occasional concentrations as rich as 2000 c.c.

The familiar fact that the mackerel are thin when they first appear near our coasts in spring, but soon gain fat on the diet afforded by the local plankton, is sufficient evidence that average volumes of this general order of magnitude, at the level of greatest abundance, corresponding to 1.2–2.2 c.c. per cubic meter of water, are more than sufficient for the maintenance and growth requirements of this particular fish. They contrast with an average of only about 300 c.c., and maximum of 914 c.c. for June and July, inshore in the southern sector.

By the evidence of 1931, the amount of nutritive plankton—however estimated—greatly decreases all along the offshore belt between July and October, to an average so low (perhaps 200–300 c.c.) that autumnal feeding conditions must be classed as moderate at best. But we have no information, under the present heading, for the late autumn or early winter.

Consideration of the relative frequency with which the plankton averaged more than twice as voluminous shoal (< 10 meters) as deep (> 18–20 meters) or the reverse, in different months, shows that mackerel, or other fish would find the best feeding conditions as often at one depth as at another during February, April, and May, while more often still, there is no strong gradient of either order at this season. By July, however, when the plankton as a whole averages most abundant in mid-depths (p. 218), the best feeding conditions would be found 15–20 times as often at some depth greater than 20 meters as between 10 meters and the surface. And on the few occasions (total cases, 24) when a very strong concentration was recorded at any particular depth (volume more than 10 times as great at one level as at another), this occurred about 5 times as often deep as shoal, for the months, February–June, but at least 20 times as often deep as shoal in July. Thus, there is nothing in the vertical distribution of the more nutritious plankton that might tend to hold the fishes subsisting upon the latter at any one depth more than at any other, from the end of winter through spring and into the first month of summer. But if plankton-eating fishes are able to find their way to the zones where food is most plentiful—which it is likely that they can vertically—they would naturally tend to desert the superficial 10–20 meters of water in midsummer (with corresponding effect upon the fisheries), unless this descent were to bring them into temperatures unfavorably low. And this would hardly be the case for the mackerel, commercially the most important fish that subsists on the larger zooplankton in our region, for water of 12–14° appears to be entirely suitable for it.

The frequency with which the hauls have yielded odd specimens of mysids (chiefly *Neomysis americana* and *Erythrops erythophthalma*), bottom living shrimps (Crago), gammarids, and cumaceans, occasionally in volumes as great as 20–25 c.c. or more, further indicates that recruitment of the plankton near the sea floor from this source provides an important additional food supply for any plankton-eating fishes that may forage close to the bottom, a category to which the local species of hake (Urophycis)—well known "shrimp eaters"—doubtless belong. And we find a still more arresting example of this sort in the Gulf of Maine in a great abundance of the edible shrimp, *Pandalus borealis*, over muddy bottoms (Hjort and Ruud, 1938; Bigelow and Schroeder, 1939).

There has been much discussion (with wide disagreement) of the extent to which fishes of various species that subsist on animal plankton direct their wanderings to follow the richest aggregations of available feed. The opportunity afforded by the records of 1930 to compare the location of the chief mackerel fishery from month to month (supplied by Mr. O. E. Sette, of the U. S. Bureau of Fisheries), with the areas where nutritive plankton was most abundant is, therefore, timely, this having been a season when both mackerel and plankton were at least moderately abundant, and when the latter was composed almost entirely of the more nutritious groups. In that particular year, mackerel were first caught in abundance in the last week of April, off Delaware Bay and southward, where the average amount of plankton had recently risen from about 180 c.c. to about 500 c.c. for the water column as a whole (Fig. 14). Prior to the first of that May, the northward extension of the rich belt of plankton seems to have been barren of mackerel or nearly so. But the fishery (following the schools of mackerel sighted at the surface) shifted northward by the middle of May to a belt extending all along from New York, eastward to Nantucket, suggesting that the mackerel that had first struck in well to the south, had migrated northward and eastward along the belt of rich feeding (> 500 c.c. of plankton), leaving behind the richest pool of all. And by July, the main body of mackerel—or at least that supporting the seine-fishery—had moved still farther east, to the region of Nantucket Shoals and the neighboring parts of the Gulf of Maine, although volumes of 1100–1600 c.c. of plankton for the water column as a whole still existed locally, in the region which they had recently deserted, with a strong probability that the whole sector between the New York and Martha's Vineyard profiles still supported an average volume of at least 700 c.c. at the most productive level.

At this point, we should remind the reader that the purse-seine fishery for mackerel, to which the present discussion is limited, draws only from such schools as are close enough to the surface to be seen, which leaves open the possibility that considerable bodies of mackerel may have remained in the eastern sector of our area that summer, after the surface schooling fish had moved farther eastward, but living deep down in the water where we have good reason to believe that the plankton was most abundant. Nevertheless, the evidence outlined above seems to us strong, that at least a large proportion of the mackerel stock travelled horizontally along the belt of abundant plankton, seemingly without reference to the precise localities where the latter was richest, to waters where we have no

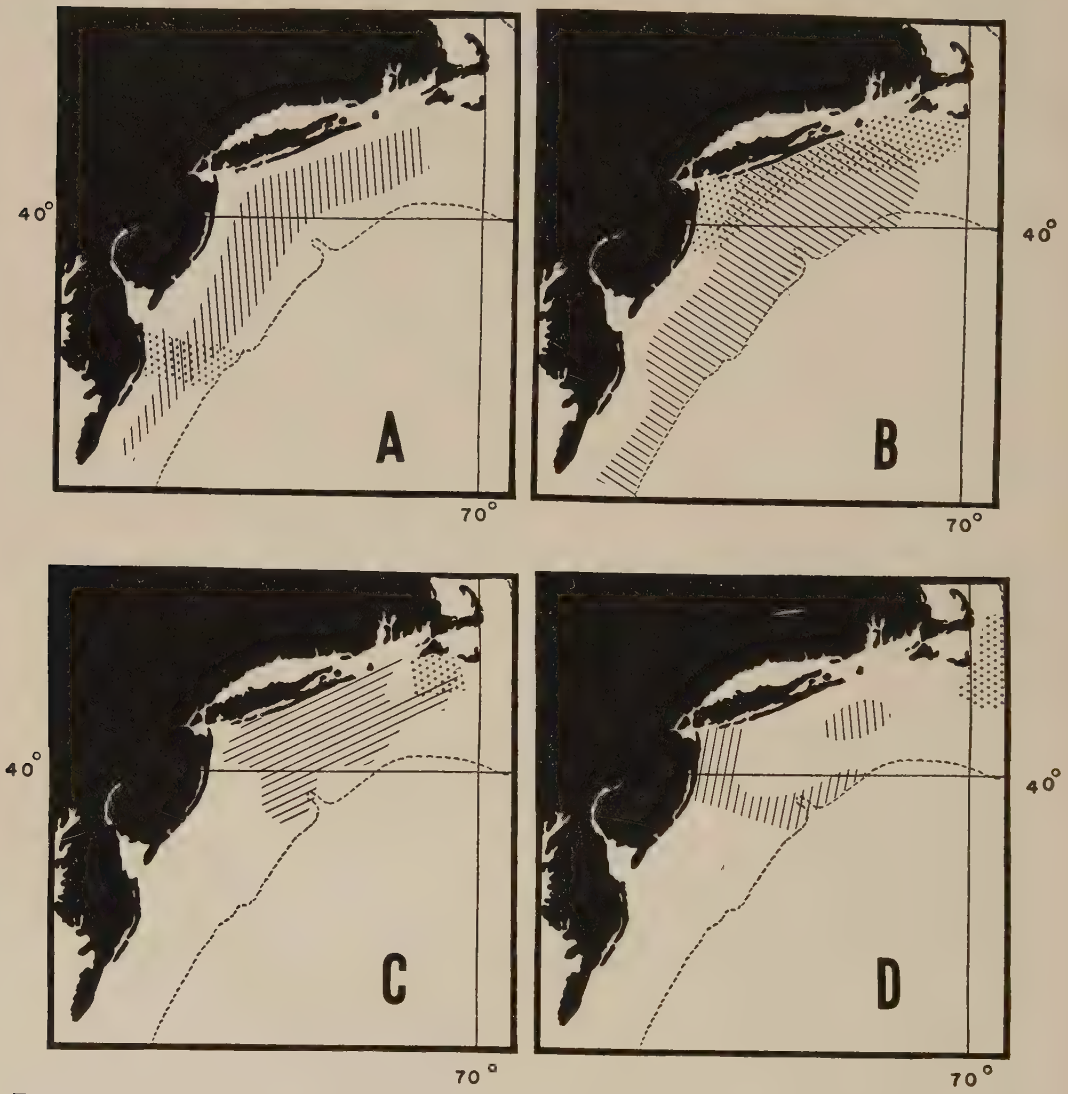


Fig. 14. Locations of areas where plankton was most abundant (hatched); and where the mackerel fishery was chiefly concentrated (dotted), in 1930: A, April 22–May 1; B, May 12–23; C, June 24–July 1; D, July 10–18.

reason to suppose that feeding conditions averaged any better; a movement for which the quantitative distribution of the plankton does not offer any apparent explanation and which must therefore be credited to some impulse to migration of a different sort.

In this respect, the mackerel may differ from the herring, for Wimpenny (1929, p. 10) remarks that the "view that herring seeks and perhaps depends upon, the fattest food seems to me to have much to commend it."

CONCLUSIONS

The Plankton as a Whole

Horizontal Distribution

The preceding discussion may be summarized as follows:

In years when the shelf waters as a whole experience a pronounced winter chilling, the zooplankton is volumetrically at a low ebb in February, though we have yet to learn whether the annual minimum falls in that month or earlier in the winter. The plankton then averages richest next the coast, and in the south, poorest in the northeastern sector and along the edge of the continent. Experience in 1930 and 1931—presumably the situation was essentially similar in 1929—suggests, as a reasonable expectation for a normal February, volumes ranging from about 100 to 500 c.c., for the water column as a whole (occasionally as rich as 1000 c.c.) in the belt marked A on Fig. 2, with averages of 150–200 c.c., of 50–100 c.c., and of 10–120 c.c. in the belts B, C, and D, respectively. And available data show that the water is notably barren, then, along the continental slope—a maximum of only 35 c.c., a minimum of 13 c.c., for all years combined.

After a warm winter, however, such as that of 1932, the late February plankton may average from two to three times as plentiful in the southern sector as in cooler years, but not significantly richer in the northern sector, so that the regional contrast at this season is widest in years of that type.

A marked augmentation in the volume of plankton takes place during the spring in some years (illustrated by 1930 and 1931), but not in others, e.g., 1929, 1932, but we still lack a convincing explanation for the existence of these two contrasting states. In years when this augmentation does occur, it appears first at scattered rich centers, as a result of which the plankton may vary widely in amount between neighboring localities. These centers may soon merge, so that the productive areas become rather sharply demarked from the less productive, as in 1930, or they may continue more or less independent, resulting in a decidedly complex areal pattern, as in 1931 (Fig. 4).

In years when vernal augmentation occurs, it is first centered chiefly in the northern and northeastern sector, expanding eastward at some time during the spring to the limit of our area (Martha's Vineyard profile) in years of high production (e.g., 1930, 1931). And it also tends to spread progressively from north to south with the advance of spring, most markedly along the mid-belt of the shelf, but also involving the waters seaward to some extent out beyond the continental edge. Vernal augmentation of this type may either culminate in May, followed by some decrease in early June, with little further alteration through July (as in 1930), or the plankton may continue to increase slowly in amount through June and into July, as in 1931. Contrasting with this enrichment to the north, and offshore to the south, the plankton of the coastal belt south of New York, at most increases slightly during the spring, as happened in 1931, or it may even decrease somewhat, as in 1930. Neither have rich pools such as may exist close to the mouth of Chesapeake Bay or southward of the latter in February or in April, ever been found there in May or later.

Various lines of evidence indicate that vernal augmentation in our area results chiefly from local reproduction, with mass immigration from the east contributing very little; indrafts of water from that source may even tend toward impoverishment.

In years of the opposite type (e.g., 1929, 1932), the plankton alters but little in average volume (continuing relatively poor) from late winter or early spring through June, as in 1932, or even through July, as in 1929. Conditions in 1932 suggest that a poor production of plankton is to be expected after an abnormally warm winter—even if this thermal abnormality be obliterated during the spring, and if summer temperatures be about normal. But—by the evidence of 1929—production may also be poor after a normally cold winter.

Since the observational series included as many years of the one type, as of the other, so far as production of plankton is concerned, the following monthly averages, for all years combined, are probably a fair representation of the characteristic state. On this basis, the volume of plankton may be expected perhaps to double over the area as a whole between February and May or June, and to multiply more than six-fold in the northern sector between February and July, in an average year, while in a year of good production, it may multiply nearly four-fold over the area as a whole, and more than 14-fold in the north, between the end of winter and the date of the summer peak. Peaks of equal abundance may perhaps develop locally in August and September when quantitative data are lacking. But the plankton then decreases again by October, to a volume about equalling the average for April.

Average volumes, c.c. per standard haul

Month	Inshore	Offshore	North	South	Area surveyed
February	339	80	75	282	222
April	252	335	354	234	231
May	342	576	451	425	443
June	343	421	388	330	372
July	551[1]	492[1]	505	—	—
October 1931	—	234	236[2]	231[2]	—

[1] North only.

[2] Offshore only.

The tabulation further shows, first, that regional contrasts are much the widest in February, when the plankton has averaged some four times as rich inshore and south, as offshore and north, and, second, that a reversal tends to take place early in the spring, from the winter state, to a slight contrast of the opposite sense (richest offshore and north), which prevails generally through April, May, and June. And the majority of the chief centers of abundance (> 900 c.c.) have similarly been concentrated on the outer part of the shelf to the north and east

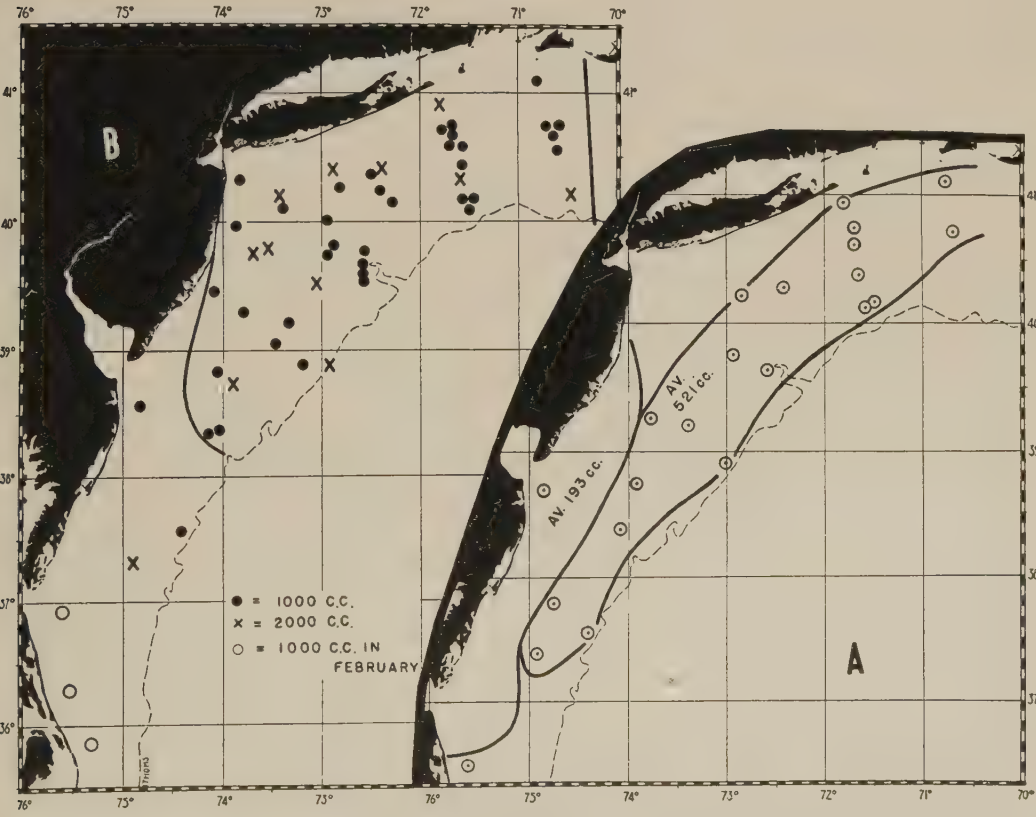


Fig. 15. Volumes of plankton: A, averages in different areas, mid-May to mid-June, of all years combined; with locations of volume greater than 900 cc.; B, stations where the volume of Plankton was larger than 1000 cc. at the richest level, after subtraction of medusae and salps.

of the Hog Island profile (Fig. 15A). But there have been considerable variations in this respect among individual cruises.

It is probable that the average volume of plankton existing in the offshore belt in the north in July 1931 (912 c.c.) approximates the maximum that is to be expected over any considerable part of our area, at any season, in normal years, though the richest catch of all (67109 c.c., mostly salps off Delaware Bay, July 18, 1929) was made at the edge of the continental shelf. At the other extreme, the region that has proved least productive in late spring and summer is the coastwise belt southward from Barnegat, where volumes from mid-May to June have averaged only about 193 c.c. Very rich centers (> 900 c.c.) may, however, develop locally, in this barren zone, as they do elsewhere (Fig. 15A).

In October, to judge from 1931, volumes average about as large north as south.[1] But we have no information as to the regional gradients later in the autumn, or in early or mid-winter.

Vertical Distribution

At the end of the winter, the plankton averages considerably richer in the upper 25–30 meters than deeper, but it is distributed with comparative uniformity, vertically, within that stratum, nor do diurnal migrations greatly affect the mass distribution at that season, when turbulence is still active, and illumination relatively weak. Migrations of this type, of the community as a whole, upward by night and downward by day have, however, proved widespread from April through June. The center of population also tends—though quite independent of this phenomenon—to sink to the mid-depths by April, there to continue through the later spring and summer. And this type of vertical stratification greatly intensifies from June to (probably) a maximum in July, when the 20–30 meter level stratum has averaged from 10–26 times as productive of plankton as the superficial 10 meters in different years. This enrichment of the deeper waters, relative to the surface, which is confined to the upper 40 meters or so, until June, also extends downward below 60 meters by midsummer.

It is probable that the development of this type of vertical stratification in spring results chiefly from the alteration usual at this season from dominance of the community by Centropages and Limacina, to dominance by Calanus. But the intensification of stratification that takes place from June to July results from the fact that by midsummer, the surface stratum warms to a temperature that is unfavorably high for the members of the boreal community that are the most prominent relatively at the season.

---

[1] The one October cruise was confined to the offshore belt.

Annual Differences

The fact that the plankton, over the region as a whole averaged about twice as voluminous in the richest year as in the poorest in February and about three times as voluminous in midsummer, within a period of only four years, marks our area as one subject to fluctuations in this respect, perhaps wide enough seriously to affect the welfare of plankton-eating fishes. At the end of the winter, the plankton was richest in the year (1932) when temperatures were highest, but subsequent production poor, whereas vernal augmentation was most pronounced and summer volumes largest in a year when the plankton had been very scarce in February and when winter temperatures had been normally low. But it is clear that this is not a case of simple control by temperature, for one of the years of this same thermal type (1929) was one of poor plankton production.

Comparison With Other Areas

By available data our area on the one side of the Atlantic and the southern part of the North Sea, on the other, rank together in volume of plankton, with averages of about 0.5–0.8 c.c. per cubic meter (as estimated by the displacement method) at the season of maximum production, somewhat surpassed by more northerly European waters, but in turn ranking ahead of the Gulf of Maine, the Gulf of St. Lawrence, the Nova Scotian shelf waters, the English Channel, and the Baltic.

Relative Importance of Different Species

Recent data corroborate earlier observations that the planktonic community of our area, though quantitatively varied, is dominated by a small number of boreal species, among which the only ones that have individually formed as much as 15% of the total catch over the area as a whole in any one month have been *Calanus finmarchicus*, *Centropages typicus*, *Sagitta elegans*, *Sagitta serratodentata*, and *Limacina retroversa*. Inclusion of species that have formed 15% for one or other subdivision (though not of the whole area) on at least one survey, would add to this list euphausiids as a group, Euthemisto sp., *Metridia lucens*, *Paracalanus parvus*, *Pseudocalanus minutus*, *Aglantha digitale*, ctenophores, and salps, the latter being the only warm water derivatives that have been found to form any considerable part of the total catch, in either subdivision as a whole, on any cruise. The members of these categories (combined) have formed 89–93% of the total volume in February, 91–95% in April, 80–93% in May, 81–91% in June, and 80–95%, and 78% in October.

At the end of winter, either *Centropages typicus, Sagitta elegans,* or Limacina may be the leading item in the community (Table, p. 229). Centropages, however, and *Sagitta serratodentata* then decline so greatly in relative abundance, that they are of but minor importance in the community in late spring and early summer, while Limacina, which ranks high as late as June in some years (1930, 1932), is negligible later in the summer. On the other hand, Calanus which occupies a minor, or at most an intermediate position in February (8% on the average) so greatly increases in importance shortly thereafter that it was by far the most prominent species in each April of record, ranking also first or second (in which case it closely rivalled the leader) in May, in June, and in July of each year. Since the observational series included one year (1932) when Calanus was relatively scarce, but others (1930, 1931) when it was abundant, its combined monthly ranking for the series as a whole may be accepted as approximately representative of normal years. On this basis, Calanus with a combined percentage of about 35% for all cruises combined (for the regions surveyed), is on the whole responsible for the production of a larger volume of plankton than any other one species, its closest rivals being *Sagitta elegans*, Limacina, and *Centropages typicus*, each with 11–12%. Calanus may, in fact, be expected to form nearly, or quite ½ of the total volume of plankton, whether for the area as a whole (47%), for the northern sector (50%), or offshore (50%), from April through July. In the south, however, it reaches its maximum importance in April (47%), declining thereafter through May and June (18–22%) to July (9%) in 1929 (perhaps 10–20% in 1916 and negligible in 1913). Calanus also decreased greatly in relative importance during the early autumn—at least in the offshore belt—in the one year of record (1931), whereas Centropages so increased that it ranked first in that October, and Calanus only third or fourth (see Table, p. 229), which taken with conditions in February, suggests that Centropages probably continues much the more important of the two through later autumn and winter. The salps and ctenophores, Pleurobrachia and Mnemiopsis,—insignificant in amount earlier in the season—may practically monopolize the water over considerable areas in the mid-sector, in warm summers such as that of 1913, and be abundant there locally, even in cool (e.g., 1916, p. 370).

In the cases of the other members of the dominant group, the trend in relative importance is upward through the spring and summer in some years, but downward in others or alternately up and down.

The following tabulation of monthly percentages for the dominant species in the total community for the series as a whole may be taken as representative of the relative rankings to be expected in normal years.

Month	Calanus finmarchicus	Centropages typicus	Metridia lucens	Paracalanus parvus	Pseudocalanus minutus	Limacina retroversa	Sagitta elegans	Sagitta serratodentata	Ctenophores	Salps
February	8%	25%	7%	3%	5%	13%	15%	13%		
April	51	8	9		5	9	5	6		
May	32	4	5		4	22	20	1	3%	<1%
June	42	4	4		2	7	15	<1		2
July[1]	51	17	2		1	1	13	1		5
October[2]	7	34	7	17	2	<1	5	5		<1

[1] North only.

[2] Offshore only.

The chief seasonal contrasts, apart from the ups and downs for individual species as just outlined, is that monopolization of the waters of our area by the regularly dominant community is most nearly complete in April, May, and June; least so in February, on the one hand, and in October, on the other; also in the south in July.

Previous explorations had shown that one need journey out only a few miles from the continental edge to encounter the typical warm-oceanic communities in full strength. And occasional representatives of a considerable number of species of warm water tunicates, copepods, pteropods, amphipods, etc., were reported widespread, here and there, over our area in the summers of 1913 and 1916 (Bigelow, 1915; 1922), as well as on most of the cruises for the period, 1929–1932, most frequently in the offshore belt, as was to be expected. But it appears that a definite barrier exists—perhaps in low salinity—to mass invasion of the shelf from offshore, anywhere to the north of the latitude of Delaware Bay, for oceanic species of all species combined, have never formed as much as 1% of the plankton in the northern sector, at any season, even in the offshore belt, with the exception of salpae, which may multiply so rapidly in the high temperatures of summer that the volumes that may be found on the shelf on any particular occasion give no indication of the numbers that may previously have drifted thither. And the dominant boreal community equally monopolizes the southern sector down past the offing of Chesapeake Bay, in April, May, and June. But it becomes relatively less important in the southernmost sector by July of normal summers, and a wide variety of oceanic and southern species considerably more so there, at that time of year. This, in fact, and the north-south gradient for Calanus are the most striking regional contrast that exists within our limits at any season. And the situation in the late winter of 1931 suggests that tropical communities may be expected to dominate the shelf waters from Cape Hatteras southward, the year around.

It is difficult to determine to what extent the plankton of our area may draw from the shelf waters to the eastward—George's Bank and the Gulf of Maine—with the invasion of the cold water that often comes from that direction in spring, because the qualitative composition of the dominant communities is much the same, west as east of Cape Cod. But the distributional pictures for the leading species lead to the conclusion that even if there be some recruitment from this more eastern, and more strictly boreal source, the maintenance of the local plankton depends chiefly on local production. It is especially instructive in this connection that species definitely to be classed as northern indicators in our area, such as *Calanus hyperboreus* and *Oikopleura labradoriensis*, have invariably formed a small part of the catches (an average of 6% at most) even on occasions when they have become dispersed far and wide. And with visitors from the coastwise water to the south equally negligible in average amount even in the southern sector at all seasons, with the unique exception of the invasion of Palinurus larvae in July 1929 that is described elsewhere (p. 243), our area is primarily self-contained so far as its plankton is concerned.

Feeding Conditions for Plankton–Eating Fishes

It has long been known that the major items in the diet of the local mackerel and probably of other fishes feeding on zooplankton, are the species of crustaceans, of pteropods, and of sagittae that dominate the plankton of our area. These differ in chemical composition as discussed on page 254. But it is not possible to assign relative weights to them, as fish food, without knowledge of their relative digestibility, for different fishes. The present discussion of the richness of the area as a feeding ground is therefore based on the assumption that they can be grouped together as "nutritive," the medusae, ctenophores, and salpae being left out of consideration as of low food value.

A better index to richness from the feeding standpoint, is afforded by the volume at the richest level, than by the average for the water column as a whole, because the former to some extent expresses the relative accessibility for fishes of the available supply. Information in this regard, obtained in 1929, 1931, and 1932, when two or more hauls were made at most of the stations, combined with adjusted values for 1930 (see p. 257 for the method of adjustment) yields the following monthly volumes of the more nutritive plankton at the richest level, for all years combined:

Average monthly volumes (c.c.) of the more nutritive plankton in the different subdivisions at the richest level

Month	Inshore		Offshore		North		South		Area Surveyed	
	Per Tow	Per M³	Per Tow	Per M³	Per Tow	Per M³	Per Tow	Per M³	Per Tow	Per M³
February	408	0.7	109	0.2	114	0.2	311	0.5	288	0.5
April	333	0.6	465	0.8	292	0.5	258	0.4	327	0.6
May	423	0.8	794	1.3	586	1.0	498	0.8	556	0.9
June	478	0.8	617	1.0	563	1.0	447	0.8	508	0.9
July	951	1.6	701	1.2	791	1.3	—	—	—	—

This tabulation (and the data for the separate years on which it is based, Tables pp. 256, 257) shows the northern sector, offshore, as averaging poor in fish food at the end of winter (in some years very barren indeed), but the southern sector, inshore, as moderately productive, especially if winter chilling has been less extreme than usual (e.g., 1932). In years of this latter type, the center of abundance may even continue in the south until early summer. Usually, however, the volume of nutritive plankton so greatly increases in the northern sector during the early spring as to make this the richest part of the area by May, at latest, so to continue through July. In some years—those of high production—the vernal augmentation involves the other parts of the area as well, but in others (represented with equal frequency in the observational series), it is confined to the northern sector. The volume in the richest area at the peak season has been found to average nearly two to three times as great in a rich year (1930) as in a poor (illustrated by 1932). But these annual differences are not wide enough to obscure the general rule that the largest volumes usually develop within the area outlined in Fig. 15 and in July, when the average there has been about 1300 c.c. for the richest year and about 900 c.c. for all years combined, with local centers of abundance as rich as 2000 c.c.

A decided decrease is then to be expected—by the evidence of the one year of record—from this peak, to perhaps ½ as much nutritive plankton in the offshore belt in October. But we have no corresponding information for the inshore belt for that month, or for any part of the area in later autumn or winter.

In winter, in spring, and in the first month of summer, the most productive level for the nutritious plankton is about as often shoal as deep, while more often still there is no pronounced stratification of either order at this season. But by July, much the largest volumes occur about 15–20 times as often at depths greater than 20 meters as within 10 meters of the surface, so that feeding conditions average much the best then in the mid-depths. But we have no evidence as to the extent to which mackerel or other fish are able to profit by the opportunity provided by this type of stratification.

In the one year (1930) when the location of the chief mackerel fishery, from month to month was compared with the volumetric distribution of the more nutritious plankton, it appeared that the fish first struck in at the southerly end of the productive belt, and then moved northward and eastward along the latter (apparently indifferent to the precise localities where plankton was richest) until by July, the surface schooling portion, at least, of the mackerel stock had passed out of our area, leaving behind feeding conditions probably as rich as those of the Gulf of Maine, Nantucket Shoals, and George's Bank, to which they had repaired. But it is possible that a part of the mackerel may have remained west of Cape Cod, but living deep.

PART II. VOLUMETRIC DISTRIBUTION OF INDIVIDUAL SPECIES

CHORDATES

Doliolum sp.

Doliolum was taken in abundance midway of the shelf off Delaware Bay in the summer of 1913, with occasional specimens near land to the southward and at scattered stations along the continental edge (Bigelow, 1915). In 1929, a large catch (80 c.c.) was made off Currituck in May, and Doliolum had become generally dispersed through the southern sector by that June, so to continue through July (50% of the stations, Fig. 16A), in quantity varying from less than 1 c.c. to 82 c.c., or sufficient to make it of some importance locally in the plankton. But the most northerly record for it on the shelf during this period was off Atlantic City, proving that it was almost entirely confined to the southern sector at the time. Unfortunately, we have no information as to how late into the autumn Doliolum may have persisted on this occasion, other than that it had disappeared at some time prior to the following February. But the fact that we have no other record of Doliolum within our limits during the four year period, 1929–1932, shows that invasions by it on a broad scale are rather unusual events, the effects of which are limited for the most part to the southern sector.

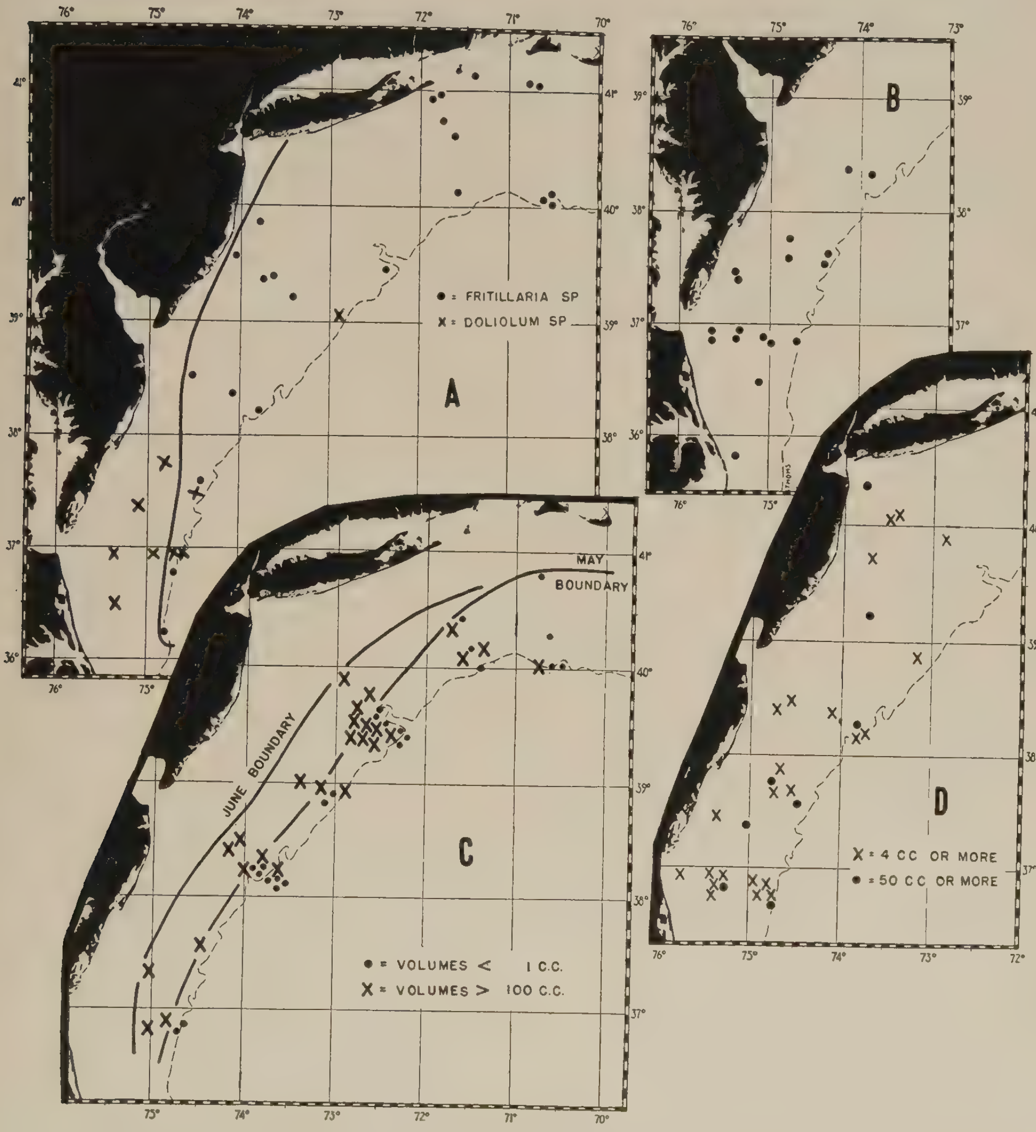

A
● = FRITILLARIA SP
X = DOLIOLUM SP
B
C
MAY BOUNDARY
JUNE BOUNDARY
● = VOLUMES < 1 C.C.
X = VOLUMES > 100 C.C.
D
X = 4 CC OR MORE
● = 50 CC OR MORE
76° 75° 74° 73° 72° 71° 70°
41° 40° 39° 38° 37° 36°

Fig. 16. Locality records:–A, Fritillaria, and Doliolum contour marking southern limit of Fritillaria; B, *Oikopleura dioica;* C, Salps; D, volumes of *Clione limacina* larger than 4 c.c.

During the height of vernal invasion in 1929 (May–July), the average volume of Doliolum was about 9 c.c. for the southern sector as a whole, the maximum about 82 c.c. And it is interesting that catches should have averaged rather higher inshore (4–5 c.c.) than offshore (1 c.c.), for Doliolum undoubtedly comes to our area from the continental slope.

SALPS

It has long been known that salps of one species or another are plentiful along the continental slope abreast of our area. And the records for 1931 show that they are to be expected in small numbers close in to the coast south of Cape Hatteras, even at the coldest time of year, while they may also occur here and there well inshore considerably farther north at the end of a warm winter, such as that of 1932, when *Iasis zonaria* was taken at three stations on the Cape May profile. But salps are either wholly wanting on the shelf north of Latitude 36° at this season in more normal years (e.g., 1930), or at least confined then (and in small volumes) to the immediate vicinity of the 200-meter contour as in 1931. And by available evidence, their status is essentially the same in April, when the only inshore record was south of Latitude 36°, though we have record of them at 10 April stations near the 200-meter line in 1930, in volumes ranging from 1 c.c. to 30 c.c., with one catch of 5000 c.c. off Montauk on the 23rd of the month in 1929. But the records for May, while equally closely confined to the continental edge in the south, are dispersed well in on the shelf in the east (Fig. 16C), in amount up to 150 c.c. By June, they have been recorded widespread in the offshore belt, south as well as north, on one cruise or another, averaging about 14 c.c. in the offshore belt (all years combined) with a maximum of 261 c.c. And by July salpae may not only occur in enormous quantities along the edge of the continent —witness a volume of some 66 liters (by rough estimate), just inside the 200-meter contour on the Cape May profile, in 1929, and another of 1046 c.c. at about the same relative situation on the Martha's Vineyard profile in 1931—but may also invade the inshore belt as well at this season, to the southward of New York in great abundance, if the summer be a warm one. This, for example, happened in 1913, when they were in swarms, along the coasts of New Jersey, Maryland, and Virginia (Bigelow, 1915, p. 275, Fig. 67), and were recorded at every station westward and southward from the Montauk profile. Small numbers of salps were even taken close in to New York in the cold summer of 1916—when tropical immigrants were at a minimum—as well as at several stations offshore, in the south (Bigelow, 1922, p. 156, Fig. 52). Conditions vary widely, however, from year to year, in this respect, apart from temperature, for the record of salps, inshore for 1929 is confined to scattered specimens at three stations, all south of New York (maximum, 5 c.c.). And we have no reason to suppose that they ever occur in abundance inshore, east of New York, even in a July when they are general and abundant farther out at sea, as they were in 1931, when the average catch of salps offshore in the north was 167 c.c. (maximum, 1046 c.c.).

Salps may persist in small or moderate numbers here and there, well in on the shelf, until October (maximum, 103 c.c.) in some years, as exemplified by 1931, most abundant and most frequent in the south as was to be expected—or even until November, when many *Iasis zonaria* were taken at two stations off Martha's Vineyard in 1916 (Bigelow, 1922, p. 157). But their status in February (p. 272) makes it likely that they vanish wholly from the shelf, to the north of Lat. 36°, with falling temperatures, at the onset of winter.

Salps may be regarded strictly as oceanic immigrants in our region, sometimes developing local swarms there under the favorable conditions of summer, but unable to maintain themselves anywhere inshore from the 200-meter contour through the cold season.

FRITILLARIA sp.

Representatives of Fritillaria were recognized at localities widely scattered across the whole breadth of the continental shelf in the northern sector, and southward along the edge of the continent as far as the Currituck profile (Fig. 16A). And while the condition of the material did not allow specific identification, i.e., whether belonging to the wide-ranging *F. borealis* or to the warm water *F. venusta* (Lohman, 1901; 1911), this distributional picture at least suggests a more northern source of supply. The seasonal distribution of the catches (11% of the stations for February, 2% for April, 7% for May, 0% for June, 3% for July, and 0% for October) would not of itself suggest any relationship to the vernal indrafts of water from the east. But the fact that the only catch of measurable volume (9 c.c.) was made in May, is at least compatible with temporary recruitment from the region of the Gulf of Maine, where Fish and Johnson (1937) found *F. borealis* in considerable frequency. Neither have we any evidence of reproduction of appreciable magnitude anywhere within our area, for all the other local records of Fritillaria were of occasional specimens only.

OIKOPLEURA DIOICA

Records for this appendicularian have been confined to the months of May (2 stations), June (4 stations), July (7 stations), and October (4 stations), and so strictly limited to the south (Fig. 16) that it can be as safely regarded as a warm water indicator in our area, as is *O. labradoriensis* of water from the east and north. In the southern sector, however, the localities of capture have been widespread, from close inshore out to the continental edge. And the fact that the catches ranged from 1–14 c.c. (average, about 8 c.c. for the stations of record) makes it likely that some local reproduction of *O. dioica* takes place as far north as Delaware Bay during the warm half of the year. But it is unlikely that this is ever on a scale large enough to make it an important item in the plankton. And we have yet to learn whether it vanishes from within our limits during the cold half of the year as completely as our failure to find it in February or in April would suggest (implying that reestablishment later in the spring depends on renewed invasion), or whether a scattering of the species actually survives the winter.

OIKOPLEURA LABRADORIENSIS

Oikopleura labradoriensis deserves attention, among the species that are usually of minor importance, both because of the wide variation in its abundance from year to year, and as an indicator of water from the north and east. It has been recorded at only three stations in February, at five in April (all in 1930), always in minimal numbers, and it may continue very scarce in some years right through the spring and early summer, as in 1930, when it was recorded at only one of the 27 stations for May, not at all in June and July. But it may increase considerably in abundance, in spring, in other years as in 1931, when (not found at all in February) it was widespread in May, over the outer parts of the shelf as a whole, southward to the offing of Delaware Bay, averaging 5 c.c. in volume, for the whole region, with a maximum of 67 c.c. And it was still more abundant in 1932, when—similarly lacking in February—it had become general throughout all but the southern part of the region by the beginning of May, averaging about 29 c.c. by the second week of the month, with a maximum of 122 c.c. This, however, represented the peak for *O. labradoriensis* in each case, for its southern boundary shifted, in 1931, from the offing of Cape May to (roughly) the offing of New York between mid-May and mid-June, while in 1932, the percentage of stations at which it occurred declined in the northern sector from 95% at the end of May to 53% by the first week in June, and to 15% by the third week of that month, by which date it was entirely confined to the extreme northeastern corner of our area, while its average volume similarly decreased in the northern sector, to an average of 4 c.c. by the end of May, and to 1 c.c. in June. We have occasional record of it only in July (8 stations, all years combined) and none at all in autumn.

Its status, thus, appears primarily to be that of an immigrant entering our area in spring, to multiply there temporarily, if conditions favor, which happens most often in May, but disappearing altogether by mid-summer.

MOLLUSCS

Clione limacina

Frequency. The records for individual cruises have shown that Clione may appear anywhere on the shelf, from the coast line out to the edge of the continent, at any time between February and October, but so irregularly and sporadically that no dependence can be placed on its presence or absence in any particular region, or at any particular time of year. Combination, however, of the records for the several cruises suggests that it is usually least frequent at the end of winter and in early spring, and that it tends to become much more so with the advance of the season, for it was taken at 11% only of the stations for February and April, but at 46% in May, 53% in June, and 32% in July, with maximum frequencies of 84%, 78%, and 50%, respectively for the last three months. And this is in line with Rathbun's (1889) report of it in about 30% of his towings between the offings of New York and of Chesapeake Bay in late April, and May of 1887. An increase in frequency through the spring was even recorded in the year (1932) when Clione was most common in February, namely from 48% of the stations in that month to 54% in May and 70% in June. And the data for 1929, when it was not taken at all in April, but at 15% and 21% of the stations in May and June, respectively, and for 1931, when it was lacking in February, but was at 37% of the stations in May, similarly suggest that in some years it may not exist at all in our area until late in the spring.

These lines of evidence mark May and June as, on the whole, the months in which Clione is most frequent, with July falling but little behind. If 1931 can be taken as representative, the species then tends to decline in frequency during the autumn, and perhaps to disappear altogether before the beginning of winter, for it was taken at 15% only of the stations in that October and not at all in November 1916.

On one cruise or another, Clione has been found most frequent inshore, offshore, in the north, and in the south, apparently independent of the time of year. It tends, however, to be somewhat more frequent offshore than inshore, for this was not only the case in eight individual months with the reverse true in five only (February, 1930, 1932; June, 1929, 1930; July, 1929), but it was also recorded at a slightly greater percentage of stations offshore (33%) than inshore (25%) for the series as a whole.

We might perhaps have reasonably expected to find a species of presumably boreal origin—such as Clione—occurring more frequently in the northern sector of our area than in the southern. Actually, it was taken at 38% of the stations in the south, but at 34% only in the north, on all cruises combined. The fact that it was wholly lacking in the northern sector in five of the individual months (February, 1931, 1932; April, May, June, 1929; October, 1931), but only in two months (February, 1930, 1931) in the southern, is in line with the foregoing. It was, again, most frequent in the south in ten of the months when both sectors were surveyed, but in two only (April, 1930; May, 1931) was it most frequent in the north. And the maximum frequency in any one month has been considerably higher south (90%, May 1930 and June, 1932) than north (66%, June 1932). Thus, there seems no escape from the conclusion that in our area, Clione must be classed as a southern species, even though this places its center of frequency close to the southern boundary to its regular occurrence. And the distribution of the richer catches is in line with this, volumes larger than 4 c.c. having been entirely restricted to the sector southward from the New York profile (Fig. 16, D), with some slight concentration of the largest volumes off Virginia and off Chesapeake Bay, while Rathbun (1889) found it "common" and "abundant" to the south, only, of Lat. 39° N., in the spring of 1887.

Percentage of stations at which *Clione limacina* was taken

Month	Year	Offshore	Inshore	North	South	Area Surveyed
February	1930	0%	9%	10%	0%	5%
	1931					
	1932	44	67	0	75	48
April	1929					
	1930	20	6	19	9	16
May	1929	15	7	0	22	15
	1930	91	66	66	91	77
	1931	70	13	50	13	37
	1932	62	45	45	71	54
June	1929	0	16	0	33	21
	1930	10	25	24	0	19
	1931	63	54	48	83	67
	1932	90	60	66	90	70
July	1929	0	25	10	22	14
	1930	20	28	23	—	23
	1931	75	23	38	—	38
October	1931	15	—	0	20	—

Average volumes of *Clione limacina*

Month	Year	Inshore	Offshore	North	South	Area Surveyed	Maximum
February	1930	<1	0	<1	0	<1	<1
	1931						
	1932	<1	<1	0	<1	<1	<1
April	1929						
	1930	<1	<1	<1	<1	<1	<1
May	1929	<1	<1	<1	<1	<1	6
	1930	<1	<1	<1	<1	<1	<1
	1931	<1	<1	<1	<1	<1	4
	1932	<1	2	<1	3	1	75
June	1929	5	<1	0	8	3	79
	1930	<1	<1	<1	0	<1	2
	1931	3	2	<1	6	3	50
	1932	5	21	3	31	12	235
July	1929	<1	0	<1	<1	<1	<1
	1930	7	<1	3	—	3	50
	1931	<1	<1	<1	—	<1	<1
October	1931	—	<1	0	<1	<1	<1

Abundance. The records of Clione in February and April, have, in every case, been based on volumes smaller than 1 c.c. And even in May, when this pteropod is approaching its maximum frequency, the average catch for the area as a whole still continued less than 1 c.c. in three of the years (1929, 1930, 1931), and was only 1 c.c. in the fourth (1932). But the maximum had risen to 4–6 c.c. by that month in 1929 and 1931; 1932 yielded six May catches of 5–10 c.c. with one of 75 c.c., while the average volume of Clione was about 5 c.c., for the area as a whole in June of the several years combined, with maxima of 50 c.c. in 1931, of 79 c.c. in 1929, and of 235 c.c. in 1932. Thus, it appears that this pteropod may be expected to experience a considerable vernal augmentation in our waters in most years, either accompanying or briefly succeeding the seasonal increase in its frequency of occurrence. If it be scarce in June, it may considerably increase soon after, as happened in 1930, when the averages and maxima rose from less than 1 c.c. and 2 c.c. in that month to 3 c.c. and 50 c.c. in July. It may even be rather numerous locally, as late as August in cool summers—e.g., 1916 (Bigelow, 1922, p. 156). It seems more usual, however, for it to be in very small volume, anywhere west or south from Cape Cod by midsummer, even if widely dispersed then, as was the case in 1931; or even lacking altogether, as seems to have been the case in 1913. And the fact that the maximum catch for October was less than 1 c.c., added to our failure to find it at all in November (1916), suggests that this is equally true in autumn.

The rapidity with which the volume of Clione may alter, emphasizes the danger of generalizing, as to what is to be expected in the oft quoted "normal" year. In 1932, for example, the average fell from 27 c.c. in the first week in June, to less than 1 c.c. a few days later, but then rose to 8 c.c. in the third week of the month, with a corresponding fluctuation in the maximum catch. But the data suggest that a maximum catch of, say, upwards of 200 c.c. may be regarded as exceptionally rich for Clione, at any season, or an average of more than 20 c.c., whether for the area as a whole, or for any considerable subdivision of the same.

Source of the local stock. The abruptness with which fluctuations take place in the abundance and frequency of occurrence of Clione, added to the fact that one year may be richest in this pteropod in one month, another year in another, introduces the question, whether maintenance in our area depends more on local reproduction or on waves of immigration. The probability has already been mentioned (Bigelow, 1922, p. 174), that local centers for this species are the result of temporary breeding activity "of such few specimens as from time to time stray southward past Cape Cod." And if this pteropod does actually vanish as completely from our scene in autumn as now appears to be the case, this early suggestion is no doubt correct. Failure to detect any larvae, on the February or April cruises, makes it unlikely that breeding takes place in our area in winter, or in early spring. It is certain, however, that widespread reproduction may occur in late spring and early summer, because larvae were taken at 27% of the stations for May and 38% for June in 1929, 75% in May in 1930, and 50% in May and 28% in June in 1932. But the situation in this respect evidently varies widely from year to year, for larvae were detected at three stations only (all in May) in 1931. Nor have we any evidence,—in the occurrence of larvae—of reproduction later than June in any year, anywhere west of Cape Cod.

In good breeding years, such as 1929, 1930, and 1932, the production of larvae is widespread over the area as a whole, at the height of the season, without apparent concentration in any particular region, except perhaps, from the New York profile southward, as contrasted with the sector farther to the east. But it appears that the offing of Chesapeake Bay is roughly the southern boundary to their presence.

In most instances, the records for larvae have been based on less than 1 c.c. per catch, except during the first June cruise of 1932, when half a dozen catches were made larger than 15 c.c., with a maximum of 73 c.c. bringing the general average for the area up to 27 c.c. It is particularly interesting—if difficult to explain—that the largest catch for this cruise (for the entire series for that matter) was made in the south, off Chesapeake Bay.

Limacina retroversa

Frequency. It seems that the southern boundary to the regular occurrence of this well known boreal pteropod is not far from Latitude 36° N., for it was not found near Cape Hatteras, on the one cruise (February 1931) that extended so far in that direction. But it has been taken widespread throughout our area to the northward of Chesapeake Bay, on one occasion or another. At any given time, its range may cover all parts of the area indifferently—as was the case in May 1932—it may be confined to a definite pool or pools, leaving other extensive areas bare, as in that same month in 1929, or it may fail altogether at one station, but prove extremely numerous at another, only a few miles distant, with rich and barren centers complexly intermingled. But its presence at 58% of the stations inshore, 50% offshore, 56% in the north, and 59% in the south, shows it as about as frequent (relatively) in one subdivision as in another.

Seasonally, however, a rather definite succession has appeared from highest frequency in February (81% of the stations) through April and May (70%), June (66%) and July (21%), for all years combined. In each year of record, furthermore, Limacina was either lacking in the easternmost sector throughout the season of observation (e.g., 1929), or showed a general tendency to disappear thence during the spring, either locally (1931, 1932), or completely (1930). It also disappeared from the south between February or April and May or June, in three of the years of record, either from the inshore belt alone (1929, 1932), or across the whole breadth of the shelf, although in the fourth year (1930), it continued general in the southern sector right through June.

The general implication of the foregoing is that in the case of Limacina, throughout the spring and early summer, a comparatively barren belt usually separates one distributional center in the Gulf of Maine, from another in the waters west of Cape Cod, centering chiefly in the general offing of New York.

If the data for October 1931, and for November 1916 can be taken as representative, two alternative explanations are open: either that adult Limacina vanishes entirely from the offshore belt—hence presumably from the area as a whole—in late summer and early autumn (it was not found at all in October), to reappear widespread as far south as Delaware Bay by November, much as Redfield (1939) reports for the Gulf of Maine, or else that a stock of adults persists right through the autumn in some years, but not in others.

No information is available in our area through the first two months of winter.

Average volumes of Limacina

Month	Year	Inshore	Offshore	North	South	Area surveyed	Maximum
February	1930 1931 1932	2 <1 228	4 <1 7	5 <1 1	1 <1 195	3 <1 138	33 2 1833
April	1929 1930	18 29	2 43	12 49	11 25	12 36	138 409
May	1929 1930 1931 1932	44 111 48 77	20 577 27 54	49 243 18 74	17 411 91 35	35 318 39 68	969 2666 400 887
June	1929 1930 1931 1932	13 84 6 12	9 16 4 40	13 74 <1 19	8 <1 16 42	12 59 6 26	220 1296 63 221
July	1929 1930 1931	6 18 24	<1 13 0	2 13 15	5 — —	3 13 15	55 128 233
October	1931	—	<1	<1	<1	<1	<1

Abundance. The great irregularity of distribution just emphasized, for Limacina, shows the danger of generalization, as to the normally seasonal cycle of abundance, or as to the average volumes of this pteropod that may be expected in different months. As an extreme illustration of variation in abundance, at a given season, we may cite February, when Limacina averaged less than 1 c.c. (maximum, less than 2 c.c.) in any subdivision of our area in 1931, but when it averaged 138 c.c. for the area as a whole, in 1932, with a maximum catch at the rate of 1833 c.c. A rather definite progression does, however, appear in the fact that the volumes of Limacina for the area as a whole averaged definitely higher in May of three of the four years (1929, 1930, 1931) than either earlier in the season or later, this seasonal peak being most clearly outlined in 1930, when it averaged five or six times more abundant in May (318 c.c.) than in April (36 c.c.), on the one hand, or in June (59 c.c.) on the other (Fig. 17). Again, in 1931, the average May catch (39 c.c.) was more than 39 times that for February, six times that for June (6 c.c.) and more than twice that for July (15 c.c.). Rich (> 100 c.c.) catches have also been made most frequently in May (17% of the stations), much

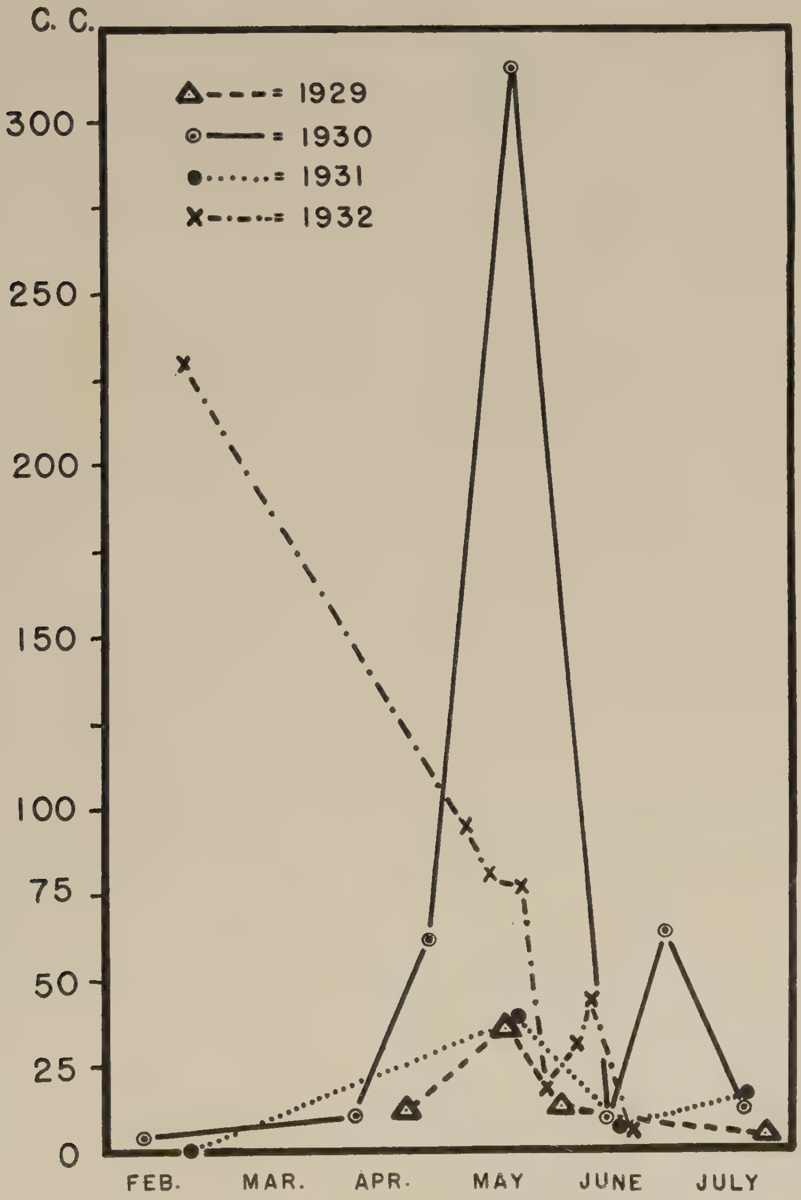


Fig. 17. Average monthly volumes of *Limacina retroversa*, in different years, for the area as a whole.

less so in February (6% of the stations), April (10%), June (6%), or July (3%), while mid- and late summer scarcity has also been recorded for 1913 and 1916 (Bigelow, 1915; 1922). But a different succession is illustrated by the data for 1932, when one very large catch (1833 c.c.) near Currituck was responsible for an average of 195 c.c. in the south, and of 138 c.c. for the area as a whole in February, but when the general average fell to 68 c.c. for May and to 26 c.c. for June.

Thus, it appears that it is usual for Limacina in our area to multiply after a normally cool winter to a pronounced vernal peak of abundance in May, then to decline as rapidly, through the summer, but that the peak may fall as early as February, after an abnormally warm winter, to be followed by progressive decrease through the spring and early summer. Present indications are that Limacina either disappears altogether for a time in early autumn, or at least continues decidedly scarce through that quarter of the year and presumably through the first two months of winter.

The volumes of Limacina have averaged about as large in one subdivision of the area as in another, for all cruises combined (average, north, 29 c.c.; south, 37 c.c.; inshore, 48 c.c. offshore, 39 c.c.). And moderately large catches have been so widespread (Fig. 18) at the season of maximum abundance (May) as to suggest that one part of the area is as likely to support a considerable population as any other. Successive cruises have, however, shown that it is characteristic for the richest centers of Limacina to be confined to small areas, and for these to shift position and extent much more rapidly from month to month than is usual with most of the other dominant members of the planktonic community.

This was illustrated in 1930 by the fact that a rich center existing near Martha's Vineyard early in April, expanded southwestward, along the mid-belt of the shelf, as far as the offing of Delaware Bay, during the next two weeks, a second rich zone having meantime developed, offshore and to the south of Chesapeake Bay, to coalesce with the more northerly center by May, followed by a contraction eastward of the resultant rich area through June (Fig. 18). Two rich centers again developed in 1931, between February and May, a larger offshore, a smaller inshore, the former to be dissipated by June, while the latter (though not encountered that month) may actually have persisted until July, when a rich catch was made at a neighboring locality. And the seasonal succession proved still more complex in 1932, when the four separate centers that were encountered during the first week of May had given place in the second and third weeks to three centers (Fig. 18), which then dispersed by the last of the month, to be replaced early in June by a fourth center, which in its turn had entirely dispersed two weeks later.

It would require a much more extensive series of observations to fit alterations as complicated and as seemingly sporadic as these into a regularly seasonal schedule, if indeed, any such applies in this case.

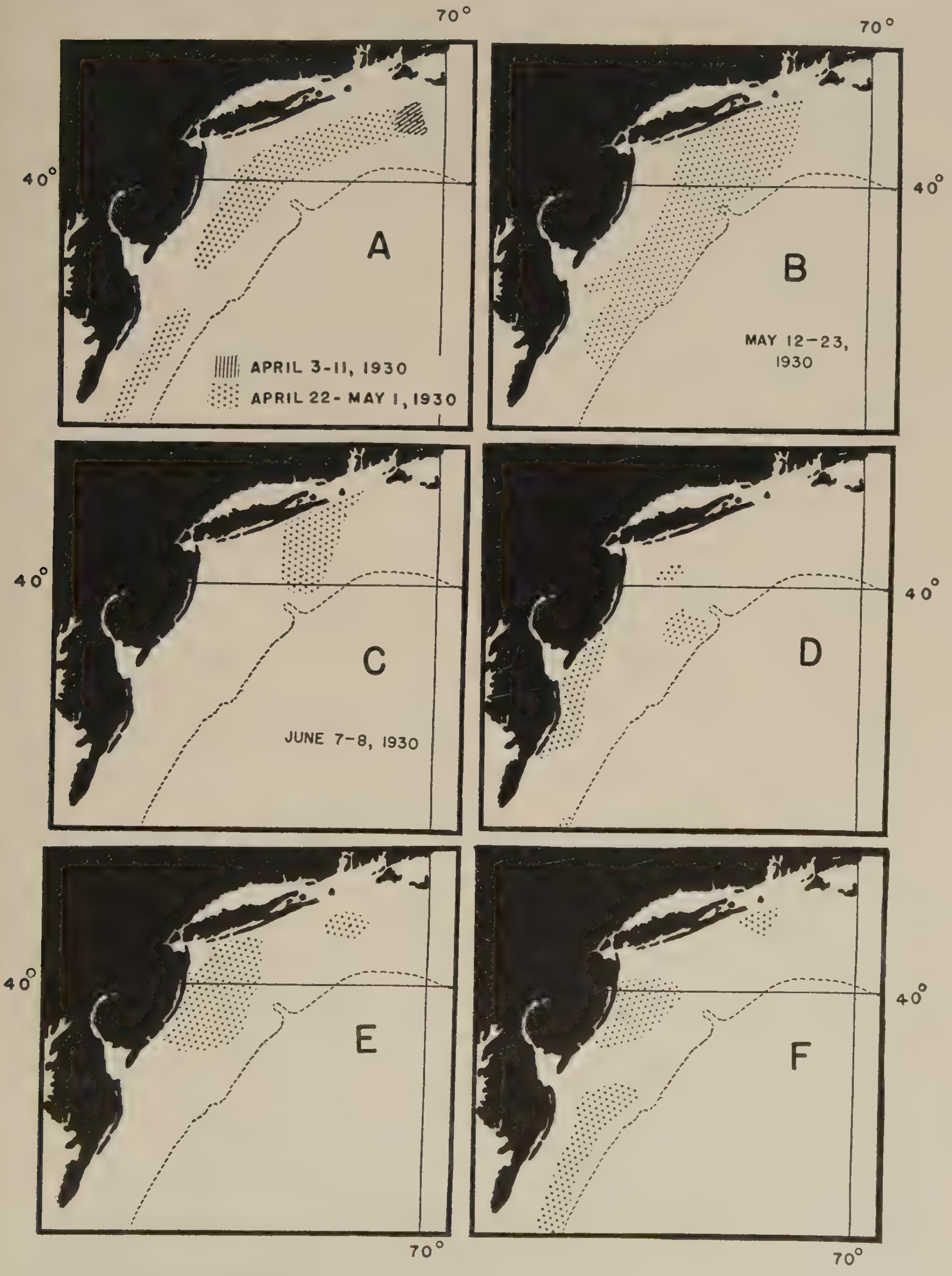

70°
40°
A
▥ APRIL 3-11, 1930
⁙ APRIL 22- MAY 1, 1930
B
MAY 12-23, 1930
C
JUNE 7-8, 1930
D
E
F

Fig. 18. Areas where the volume of *Limacina retroversa* averaged greater than 100 cc., per standard haul, in different months: A, April 3–11, 1930 and April 22–May 1, 1930; B, May 12–23, 1930; C, June 7–18, 1930; D, May 2–6, 1932; E, May 9–16, 1932: F, May 19–23, 1932.

Vertical distribution. Among the stations where tows were made at two levels, the shoal catch of Limacina was twice the larger of the pair slightly more often (55 cases) than the reverse (47 cases), though more frequently (97 cases), the two did not differ significantly, one from the other. The volumes also averaged slightly larger (average, 53.5 c.c., 200 cases), for hauls centering shoaler than 10 meters than for those centering deeper than 20 meters (average, 37.8 c.c., 201 cases).

Perhaps more significant is the fact that five of the seven catches greater than 400 c.c, that were made at pertinent stations, were from the shoaler, only two from the deeper haul, suggesting that centers for Limacina are more subject to transport by temporary wind-drifts than in the cases of species for which the centers of abundance lie deeper.

Relation to temperature. The data do not warrant any general comparison between average catch and the temperature of the water. It appears, however, that values higher than about 18° are not favorable for Limacina, for while the catch of the shoal hauls averaged about 27 c.c. in June and July as a whole, it averaged only about 5 c.c. (including one catch of 81 c.c.), at the group of stations where the upper 10 meters was warmer than 18°.

Annual variations. Average volumes for the period, February-June, were 5–6 times as great in the most productive years of the series (average, about 100 c.c. in 1930, and about 71 c.c. in 1932), as in the poorest (14 c.c., 1931). And it is not unlikely that a longer term might not have shown still wider variation, there being no warrant for assuming that any one of the four years illustrated an extreme state in either direction. *Limacina retroversa* is, in short, an extremely variable species, so far as prevailing abundance is concerned, not only from season to season, and from place to place, but also from year to year. And a similar variability is recorded for its frequency of occurrence, for while it was recorded at 83% of the stations in one of the years (1932), it was found at 51%, only, in another—1929.

Source of the local stock. Redfield's (1939) recent demonstration that the stock of Limacina in the Gulf of Maine draws—at least largely—on immigration from Nova Scotian shelf waters, and that the quantitative distribution within the Gulf is determined by the drifts undergone by the entering shoals and their offspring, opens the question to what degree this may also apply to the waters west of Cape Cod. Two lines of evidence are available, first, the presence or absence of very young stages, the implication of which is obvious, and second, the time intervals that intervened between the development of different centers of abundance, relative to their geographic locations, and to their distances apart.

The year 1930 is the member of the series in which a Gulf of Maine source might most plausibly be argued for an increase that took place between February and early April in the abundance of Limacina in the most easterly sector of our area, since the temperatures gave evidence of a coincident drift of cold water from the east, past Cape Cod (Bigelow, 1933, p. 30). But we cannot credit to this source the extension of the rich belt southward along the mid-zone of the shelf, past the offing of Chesapeake Bay, a distance of about 360 miles, (Fig. 18A), that took place between the first and third weeks of the month, unless we admit the prevalence, meantime, of a corresponding drift at the rate of at least 10 miles per day, which is forbidden, not only by navigational experience, but by the progress of vernal warming at the time (Bigelow, 1933, p. 30). And the development of rich centers, in the years, 1929, 1931, and 1932, centered chiefly in the mid-sector of our area, with little evidence of prevailing drift, whether north or south. It thus appears that if any mass immigration did take place into our area from the eastward in either year, this must have happened prior either to April (1929, 1930), or at least prior to May (1931, 1932), i.e., at a season when the stock of Limacina in the southwestern part of the Gulf of Maine and on George's Bank is low.

The evidence of the frequency of young stages among the population in April, 1930, also argues for a local source—or at least for sources not far distant, for rich centers that developed during that month, for such of the catches as were greater than 100 c.c. contained 57–86%, by number, of juveniles less than 0.6 mm. in diameter; they even contained 2–26% of specimens smaller than 0.3 mm., although the meshes of the nets used were large enough (about 0.5 mm.) to have allowed these to pass through. And rough examination has shown that considerable percentages of young specimens are also included in the rich catches for other years, which have not yet been examined in detail.

We have, in short, as good a reason for regarding Limacina as regularly and primarily endemic southward past Delaware Bay, and perhaps southward past Chesapeake Bay, as for so regarding any other member of the planktonic community.

Invasions of water past Cape Cod, would of course, add to the local population, if at a season when Limacina is abundant in the neighboring parts of the Gulf of Maine area—as would indeed, happen for any other member of the boreal assemblage. But there is no need to invoke such invasions to explain the continued presence of this pteropod within our area.

Other Molluscs

During July-August, 1913, the warm water pteropods, *Corolla calceola*, *Criseis acicula*, *C. conica*, and *C. virgula*, and the heteropod, *Firoloida desmarestia*, were taken at scattered localities on the shelf, inshore as well as offshore, from the Atlantic City profile southward: Corolla, in fact, in some abundance at one station, as described elsewhere (Bigelow, 1915, p. 302, Fig. 72). And warm water species of Limacina were again recognized at three stations, along this same sector, in the summer of 1916 (Bigelow, 1922, p. 155, Fig. 51). But our only record of this group during the period 1929–1932, was for odd specimens of tropical pteropods at one station off Bodie Island in February 1930, at one off Currituck in April of that same year, and at two on the New York profile in February 1932. These data show that it is an unusual event for members of this category to invade the shelf from offshore in numbers sufficient to be picked up in the tow nets. And the fact that they were most strongly represented in on the shelf in the summer of 1913 and again in 1916, but apparently not at all at that season in 1929, or in October 1931 (years in which the southern sector was surveyed in those months), is evidence that their temporary presence within our limits (resulting from transport by indrafts of water from the slope) is independent of precise conditions of temperature at the particular place and time where they may be encountered.

DECAPODS

Crab and hermit crab larvae

Crab or hermit crab larvae (not yet identified) were recorded at 1/3–1/5 of the stations for February, in each of the years of record, mostly over the outer half of the shelf, but indifferently from north to south, with a maximum catch of less than 1 c.c. They were slightly more general in April, when they were recorded at most of the stations in the southern sector in 1929, and scattered all along from south to north in 1930, in which year a catch of 82 c.c. near Delaware Bay on the 24th, showed that important contributions from this source, are to be expected locally, close inshore at this season (Fig. 19). And by May, crab larvae may be present in such abundance next the land as to yield catches as large as 200 c.c., as happened in 1932, though in other years (1931), their numbers may be insignificant in that month, even at inshore localities.

The catches made in successive cruises in May 1932 illustrate the wide fluctuations that may take place in their abundance within short intervals of time, for

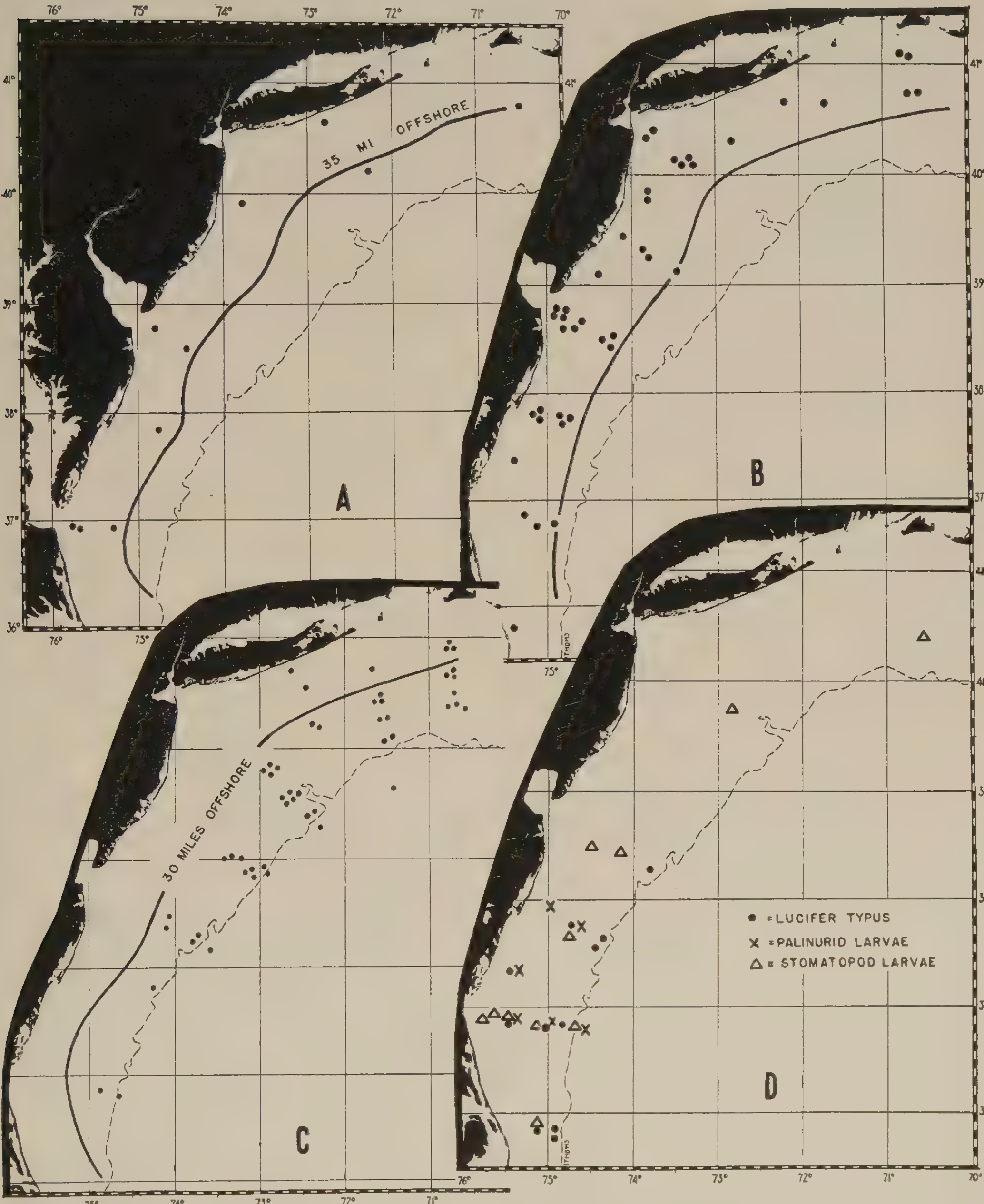

76°
75°
74°
73°
72°
71°
70°
41°
40°
39°
38°
37°
36°
35 MI OFFSHORE
A
B
30 MILES OFFSHORE
C
D
THOMS
● = LUCIFER TYPUS
X = PALINURID LARVAE
△ = STOMATOPOD LARVAE

Fig. 19. Locality records, all cruises combined: A, crab and hermit-crab larvae, volumes larger than 10 cc.; B, Crago, contour marking offshore boundary; C, euphausiid larvae, volumes larger than 25 cc; D, *Lucifer typus*, palinurid larvae and stomatopod larvae.

they practically disappeared from the whole area between the first and middle of the month, but soon reappeared in the southern sector in such abundance that catches up to 144–200 c.c. were made there during the third and fourth weeks, another center of abundance (maximum, 90 c.c.) having meantime developed near the northeastern boundary of the area. Wide variation has also been recorded from year to year in the order of change, from May through June, in the case of this heterogeneous category. The one extreme is illustrated by 1931, when they were recorded at 4 stations only in May, but had become general throughout the area by mid-June, the other extreme by 1929, when 100% frequency in May gave place to only about 50% frequency in June, while the other two years showed intermediate states, namely, a peopling of the coastal belt eastward from New York between mid-May and the first of June in 1929, contrasted with a decrease in frequency in the northern sector in 1932 from 100% of the stations in May, to only 37% in June. Until the several constituent species are studied in detail, it will be premature to postulate the order that exists in these fluctuations, beyond the two outstanding facts, (a) that crab larvae, on the whole, appeared in about twice as great frequency in June (67% of the stations), as in May (34% of the stations) for the term of years as a whole, and (b) that most of the June catches that were larger than 4 c.c., were made within 35 miles of the coast line.

The frequency of occurrence of crab larvae changed but little from June to July in 1929 or 1930. But in 1931, they had disappeared entirely by July from the northern sector, where they had been taken at 84% of the stations in the preceding month. The following tabulation also shows that they considerably decreased in volume from June to July in each of the years (1929, 1930) when they occurred in more than minimal amount in either of these months. The catches have also averaged so small in the offshore belt even at the peak season (average, 6 c.c., June 1931) as to show that the contribution made to the plankton above, by crabs living in depths greater than about 50 meters is usually negligible. And while experience in 1913 had already shown that larvae of the blue crab (Callinectes) may swarm, close in to the land near Chesapeake Bay in July (Bigelow, 1915, p. 271), we have no evidence that the product of this particular species ever adds appreciably to the plankton, for more than a few miles out from the land, though its breeding range extends northward at least to Woods Hole. No crab larvae were detected during October 1931 in the offshore belt, though they may have been present, in unknown number at the time, in the inshore belt, which was not visited during that cruise, nor have we any information for the months November-January.

The volume of crab larvae averaged about 10 times as large, for the area as a whole, in the most productive year (1931, 10 c.c.), as in the least productive (1930, 1 c.c.), in June—on the whole the peak month— while a maximum catch of 226 c.c. in 1932, contrasts with 68 c.c. in 1930.

Average volumes of crab and hermit crab larvae

Month	Year	Inshore	Offshore	North	South	Area surveyed	Maximum
February	1930	<1	<1	<1	<1	<1	<1
	1931	0	<1	0	<1	<1	<1
	1932	<1	<1	<1	<1	<1	<1
April	1929	<1	<1	<1	<1	<1	7
	1930	3	<1	<1	4	2	82
May	1929	6	<1	2	6	4	31
	1930	5	1	4	3	3	36
	1931	1	0	1	0	<1	18
	1932	13	3	2	19	8	226
June	1929	7	1	7	3	5	87
	1930	3	<1	<1	7	1	68
	1931	12	6	11	8	10	70
	1932	4	1	3	2	2	38
July	1929	2	<1	<1	1	1	10
	1930	<1	0	<1	—	<1	<1
	1931				—		
October	1931	—					

Crago sp.

The records for Crago, in late stages of development—picked up no doubt when the nets were working closest to bottom—are sufficiently general (Fig. 19B) to show that a considerable population of this familiar benthonic genus of shrimp inhabits the inshore belt, as a whole, from the one boundary of our area to the other. But one only of the records was more than 40 miles out from the coast, the great majority lying within 30 miles of the latter. Thus, it appears that the offshore boundary to the regular occurrence of Crago lies not far from the 50-meter contour, depth rather than distance from land being in all probability the determining factor.

The capture of Crago at 35% of the inshore stations in February, and 27% in April, but only 10% in May, 6% in June, and 5% in July,[1] suggests that it rises (or is swept upward) from the sea floor in significant numbers, most commonly in winter, when turbulent movements of the water are the most active, and that it does so less and less commonly, with the advance of spring and summer.

---

[1] No hauls were made inshore in October.

As a rule, odd specimens only were taken. Once, however, a volume of 35 c.c. of juveniles (13% of the total catch) was recorded (off New York, June 26, 1930), showing that on occasion the young stages, at any rate, of this genus may occur in the mid-depths in such abundance as to be an important item in the general planktonic community. And the fact that adults were so often picked up in our nets, suggests that—being of considerable size—they may be an important source of food for fish foraging near the bottom well out on the shelf, as has long been known to be true in shallow water near shore.

Palinurid larvae

The northern boundary to the normal range of the adult spiny lobster (*Panulirus argus*) along the American coast, lies some 120 miles south of the southern limits of our area. But it has long been known that the curious leaf-like "Phyllosome" larvae, probably of this parentage, often stray far to the northward with the general drift of the so-called Gulf Stream, as do many other tropical animals. Consequently, it would not be astonishing should odd specimens be carried here and there across the continental edge, in summer, when the surface waters are at their warmest. Actually, however, we have record of only one such incursion, namely, in July 1929, when the larvae were found in amounts varying from 1 c.c. to 9 c.c. at 6 out of the 9 stations that were occupied south of Delaware Bay (Fig. 19D), but when they seem entirely to have been confined to the southernmost sector.

Lucifer typus

The only decapod, apart from crab larvae, Crago, and palinurid larvae that has been detected in the catches, is *Lucifer typus*, a visitor from offshore. Lucifer was taken at two stations in February (1930, 1932), at one station in April (1930), three stations in June (1932), and five stations in July (1929), always in the southern sector as accords with its warm water origin (Fig. 19D). One catch of 23 c.c. was recorded in July 1929, one of 8 c.c. in that same month, and another of 8 c.c. in April, the other records being based on odd individuals only. There is nothing in this record to suggest that Lucifer is ever of volumetric importance within our area, even in the southernmost sector.

STOMATOPODS

Occasional stomatopod larvae were recorded in February (1 station), May (1 station), June (3 stations), and July (7 stations) at the localities shown on

Fig. 19D; also near the outer edge of the shelf, on the Winterquarter profile, in July, 1913 (Bigelow, 1915, p. 271).

EUPHAUSIIDS

MEGANYCTIPHANES NORVEGICA

Meganyctiphanes norvegica is an offshore and northern species in our area (Table, p. 292) as was to be expected. In February and April, its area of occurrence southward from the offing of Atlantic City has in fact been definitely confined to the outer part of the shelf (Fig. 20), while it was found only once inshore

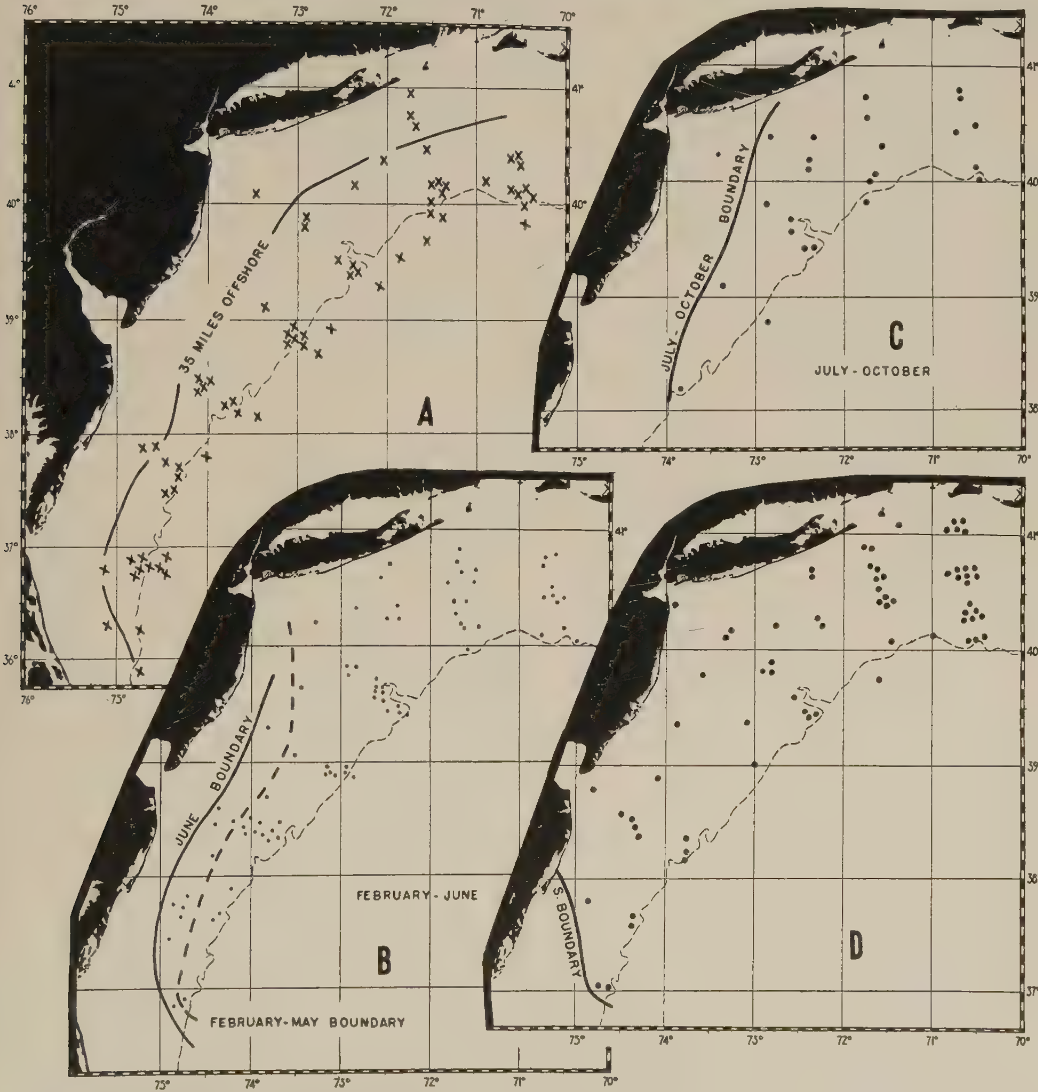

76°
75°
74°
73°
72°
71°
70°
41°
40°
39°
38°
37°
36°
35 MILES OFFSHORE
A
JULY - OCTOBER BOUNDARY
C
JULY - OCTOBER
JUNE BOUNDARY
FEBRUARY - JUNE
B
FEBRUARY-MAY BOUNDARY
S. BOUNDARY
D

Fig. 20. Locality records, all cruises combined: A, *Nematoscelis megalops;* B, *Meganyctiphanes norvegica*, February-June; C, *Meganyctiphanes norvegica*, July and October; D, *Thysanoessa inermis*.

in May of either year. And though some slight dispersal, toward the land, seems to have taken place, in June in 1931 and 1932 it was wholly lacking inshore or in the south in June and July 1929, though present then at about 50% of the stations offshore, in the north.

In the northern sector offshore, it has averaged about as frequent in one month as in another, from February to June over the term of years. Its status there varies widely, however, in midsummer, from year to year, the one extreme being illustrated by 1929, 1930, and 1932, when it was about as frequent in July as in June, the other by 1913 and 1916, when it was not found at all in July-August inside the 200-meter contour. Neither is any correlation apparent between its presence or absence at this season, and the prevailing temperature, for one of the summers when it failed (1916), was notably cold in this part of the sea, the other (1913), warm. And the danger of confusing annual variations with seasonal makes us cautious in drawing from the tabulation of monthly averages the obvious inference that Meganyctiphanes tends to spread southward along the offshore belt, and inshore, in May and June, to vanish thence with the advance of summer.

Percent of stations at which Meganyctiphanes
was taken, all years combined

Month	Offshore North	Offshore South	Inshore North	Inshore South
February	33%	0%	0%	0%
April	25	0	0	0
May	27	44	7	0
June	40	60	13	22
July	55	0	7	0
October	25	20	—	—

The records of capture of Meganyctiphanes in October of 1931 (Table, p. 293) suggest that in a year when it is widespread (at least in the northern sector) in summer, a scattering population may be expected to persist all along the offshore belt through the autumn.[1] But it appears that in years when it is absent in late summer, reestablishment is not to be expected during the subsequent autumn, and perhaps not until the following spring, for in 1916—a year of that type—it was not found at all in November whether inshore or offshore. It is unfortunate, in this connection, that no information is available as to the status of this euphausiid during the autumn of 1929, a year when it was widespread offshore in July.

---

[1] No inshore data for that cruise.

The following tabulation suggests that it is characteristic (if not invariable) for Meganyctiphanes to increase somewhat in average abundance, and still more in maximum abundance, from a minimum in February and April, to a maximum in late spring or early summer, though perhaps never to an extent sufficient to make it of more than a very minor item in the general community of our area. In some years this vernal augmentation may culminate, as a more or less definite peak in June (1929, 1931), with a subsequent impoverishment by July. And it is possible that 1913 and 1916 represent the extreme in this direction, i.e., entire disappearance in summer, but our lack of information, earlier in the season, for either of these years leaves this an open question. In other years, e.g., 1930, Meganyctiphanes, while averaging somewhat less abundant in June than in May, may average about as abundant in July as in June, at least in the northern sector, or again, there may be no significant alteration in this respect between May and June (e.g., 1932).

In any case, the small volumes recorded for October 1931, combined with the fact that Meganyctiphanes was not taken at all in November 1916, suggest that this euphausiid may be expected to decrease in abundance through the autumn, or even to disappear entirely from our waters by that time, if it has not already done so earlier in the season.

Average and maximum volumes of Meganyctiphanes, all cruises combined

	Offshore North		Offshore South		Inshore North		Inshore South	
Month	Average	Maximum	Average	Maximum	Average	Maximum	Average	Maximum
February	<1	<1	0	0	0	0	0	0
April	<1	<1	0	0	0	0	0	0
May	<1	18	1	39	<1	<1	<1	<1
June	5	89	1	16	<1	18	1	43
July	1	10	0	0	<1	5	0	0
October	1	1	1	1	—	—	—	—

NEMATOSCELIS MEGALOPS

Records of the occurrence of *Nematoscelis megalops* on the continental shelf are interesting chiefly because this euphausiid may safely be regarded as an indicator of water from the continental slope. The fact that 48 of the 59 stations where it has been taken within our limits on one cruise or another have been more than 30 miles out from the land, and most of them near the continental edge (Fig. 20A), accords with its oceanic origin. And it occurred about as frequently offshore in the one sector as in the other (18% of the stations north, 25% south, all cruises combined).

Nematoscelis was taken at 20% of the stations on the outer half of the continental shelf in February, 15% in April, 15% in May, 23% in June, 6% in July, and 25% in October, suggesting some tendency toward temporary withdrawal in midsummer, corresponding to which it was not found at all inside the 200-meter contour in July-August of 1913 or of 1916, though it was recorded over the continental slope in both these summers. And seemingly it is more likely to stray inshore in June, than either earlier or later in the season, for the distribution of inshore records (1929–1932) was February, 0; April, 0; May, 1; June, 4; July, 1.

In the great majority of cases the catches of Nematoscelis in on the continental shelf have been smaller than 1 c.c., the only notable exceptions being the following:

February, 1930, average, offshore, 5–6 c.c., maximum, 34 c.c.,
April, 1929, average, offshore, 1–2 c.c., maximum, 23 c.c.,
May, 1932, 1 station, 60 c.c.
June, 1929, average offshore, 1 c.c., maximum, 13 c.c.,
June, 1932, average offshore, 2 c.c., maximum, 28 c.c.

Catches larger than 10 c.c. were made at two offshore stations in February, none in April, two in May, five in June, and none in July and October, a distribution suggesting that when scattered centers of moderate abundance do develop for this species, this is more apt to happen in summer or early autumn than in winter, spring, or late autumn. And the largest volumes of all (34 c.c., February 11, 1930; 60 c.c., May 9, 1932) were encountered in the southernmost sector off Bodie Island, and off Chesapeake Bay.

Nematoscelis—like most other planktonic species—varies considerably in its status in our waters from year to year, catches of 10 c.c. or larger having been made at two offshore stations in 1929, one in 1930, none in 1931, and six in 1932.

THYSANOESSA INERMIS

Frequency. Discussion of the status of *Th. inermis* is hampered by the fact that in many cases, the catches of euphausiids were so damaged that it was not possible to carry identifications of the members of Thysanoessa farther than to their genus. The following estimate of the local abundance of *Th. inermis* must therefore be regarded as minimal—actually its importance was no doubt greater. Even allowing for this, it is, however, clear that adult *Th. inermis* occurs much less regularly in our area (detected at only 13% of the stations) than in the Gulf of Maine, where it has been recorded at about 50% of the stations where euphausiids were identified, summer and winter alike (Bigelow, 1926, p. 136). Nevertheless, the localities of record are so widespread (Fig. 20D) that *Th. inermis* is evidently to be expected anywhere within our area, at one time or another, south even past the offing of Chesapeake Bay.

Averages for different months indicate considerably greater frequency for July (33% of the stations) and October (25%) than for February (9%), April (4%), May (8%), or June (10%). But we must remind the reader that this applies only to the adults;—inclusion of the juveniles (which have not yet been identified) might result in quite a different seasonal picture. *Th. inermis* has also averaged more frequent in the north (15% of the stations) than in the south (5%), as was to be expected. In fact, it was recorded only twice south of Chesapeake Bay. And it also proved more frequent offshore (13% of the stations) than within 30 miles of the land (9% of the stations).

Abundance. The catches of adult *Th. inermis* have invariably been insignificant compared with those of the volumetrically more important species, the maximum being only 20 c.c. (Station, Shinnecock II, June 12, 1931), with 1.5 c.c. as the largest average for any one cruise (July 1930), while the species was not detected at all in the catches on two of the cruises (February 1932 and June 1929). This prevailing scarcity within our limits of adults of this species is an interesting contrast to the important rôle in the planktonic community that it often plays in higher latitudes, in both sides of the Atlantic.

Th. inermis was about 20 times as frequent in the richest year (1931, 40% of the stations), as in the poorest (1929, 2%). But the volumes have invariably been too small to warrant any statement as to annual variations in abundance.

THYSANOESSA GREGARIA

Occasional adult specimens of *Th. gregaria* were taken in February 1932 at stations scattered from the northern boundary of the area to the southern (Fig. 21A). Other than this the recent record of the species in our area is confined to one station off New York in May, 1929, and a second off Block Island in February, 1931), both near the 200-meter line. These localities show a distinctly southern distribution, as was to be expected. And the numbers have, in every case been so small (invariably less than 1 c.c.) that it would evidently be exceptional for *Th.*

gregaria to form any appreciable proportion of the plankton, at least during the vernal half year.

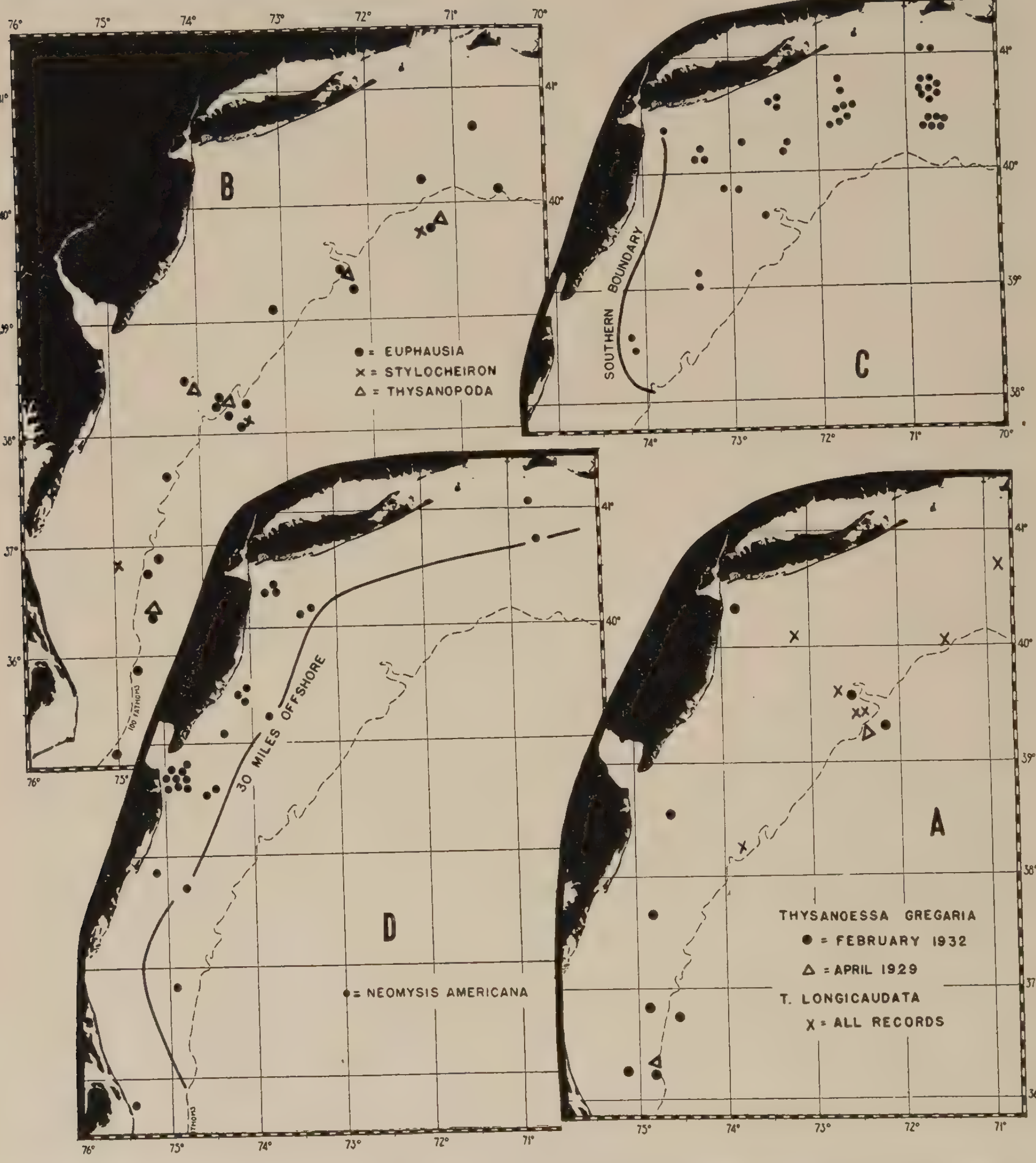

B
● = EUPHAUSIA
× = STYLOCHEIRON
△ = THYSANOPODA
100 FATHOMS
C
SOUTHERN BOUNDARY
D
30 MILES OFFSHORE
● = NEOMYSIS AMERICANA
A
THYSANOESSA GREGARIA
● = FEBRUARY 1932
△ = APRIL 1929
T. LONGICAUDATA
× = ALL RECORDS
76°
75°
74°
73°
72°
71°
70°
41°
40°
39°
38°
37°
36°

Fig. 21. Locality records, all cruises combined: A, *Thysanoessa gregaria* and *Th. longicaudata;* B, Euphausia, Stylocheiron and Thysanopoda; C, Erythrops; D, *Neomysis americana.*

Thysanoessa longicaudata

The few records for this cold water species—3 for February and 3 for June of 1930, and one for February, 1932—have all been to the northward of Latitude 38° (Fig. 21A). The largest catch (Station, Cape May V, June 11, 1930) was at the rate of 7 c.c., all other records being based on odd individuals only.

Euphausiid larvae

Specific identification of the euphausiid larvae has not been attempted, but these have formed a sufficient proportion of the catches in some months (Table, p. 229) to justify some notes as to their frequency of occurrence and local abundance.

None were taken in February, though cruises were made in that month in three different years, hence we may conclude that there is no reproduction in significant amount by any of the local species of this group, in late winter. But the frequent occurrence, in April, May, June, and July, of juveniles large enough to be caught in our nets shows that one euphausiid or another may be breeding within our limits from early spring until midsummer. The monthly succession does not suggest any definitely seasonal gradient in the frequency of occurrence for larval euphausiids between April and July, other than the irregularities (regional and secular) that are to be expected in the distribution of a mixed plankton population, but they were found at one station only in October.

On different occasions, these larvae have been most generally distributed inshore, offshore, in the north, and in the south. But they have averaged considerably more frequent offshore than inshore in each month, April-July, for the several years combined, also more frequent in the north than in the south, in April, May, June, and October, for all years combined, suggesting that production in the spring and autumn is chiefly by boreal species, probably *Th. inermis* and Meganyctiphanes in combination. In July, however, of the one year when the midsummer survey covered the entire area, they were most frequent in the south.

Percentage of stations at which euphausiid larvae were taken

Year	April	May	June	July
1929	31%	40%	30%	56%
1930	53	7	15	12
1931	—	40	27	5
1932	—	54	62	—

Percentages of stations with euphausiid larvae, in the different subdivisions, all years combined

Month	Inshore	Offshore	North	South
April	24%	64%	54%	35%
May	30	62	54	25
June	33	43	42	22
July	30	30	30	66

In the years 1930 and 1931, the catches of euphausiid larvae averaged less than 1 c.c. for the area as a whole on 11 out of the 12 cruises, and only 5 c.c. (with a maximum of 60 c.c.) on the twelfth (April 22-May 1, 1930), stocks so small that they did not contribute significantly to the general volume of plankton for that pair of years. They were, however, considerably more abundant both absolutely and relatively in the other two years of the series, with average and maximum catches of 3 c.c. and 47 c.c. in April, 8 c.c. and 169 c.c. in May, 2 c.c. and 27 c.c. in June, and 6 c.c. and 118 c.c. in July, in 1929; also 8–10 c.c. and 121 c.c. in May and June, 1930. These values combined with the absence of euphausiid larvae in February and their great scarcity in the one October of record is evidence that in their years of abundance, production takes place chiefly from May into July.

The volumes of euphausiid larvae have also averaged 14 times as great offshore (average, 14 c.c.) as inshore (average, 1 c.c.), and somewhat greater in the north (8 c.c.) than in the south (about 5 c.c.), in the 8 surveys[1] (combined) for which the average was greater than 1 c.c., in either subdivision: evidence that the production of euphausiids in our area is centered chiefly along the outer belt of the shelf. And a similar segregation appears in the distribution of catches richer than 25 c.c. (Fig. 19C).

OTHER EUPHAUSIIDS

Odd specimens of Euphausia, Stylocheiron, and Thysanopoda (strays from offshore) were taken along the outer half of the shelf at the localities shown on Fig. 21B, but never in as large an amount as 1 c.c.

MYSIDS

A considerable proportion of the hauls yielded a scattering of adults of two species of mysids, *Neomysis americana* and *Erythrops erythrophthalma*. The captures of the former (Fig. 21D)—occasional specimens only—show that it is rather closely confined to the inshore belt, as was to be expected, since it is common in seaweed and swimming free in the water alongshore. And the fact that it was recorded both in the extreme south and in the extreme north of our area accords with its known distribution, coastwise, for it is plentiful near Woods Hole, on the one hand (Sumner, Osborne, and Cole, 1913), and in Chesapeake Bay, on the other (Cowles, 1930). The fact that the monthly percentage of stations in the inshore belt, where Neomysis was taken, varied only between 5% and 6% from February to July, shows it as continuing about equally frequent from late winter through summer. In Chesapeake Bay, however, Cowles found it most plentiful in December and January. And this may be equally the case along the open coast, where we have no information for early or mid-winter.

---

[1] April, May, June, July, 1929; April, June, 1930; May, June, 1932.

In the case of Erythrops, the stations of record are generally distributed over the inner and mid-belts of the shelf; all but two, however, of the 41, are in the northern sector, with evident concentration toward the northeast (Fig. 21C). In fact, the discovery of this northern species, at all, to the west of Cape Cod, considerably extends its known range in that direction, for it had not previously been recorded south of Massachusetts Bay, on the North American coast, though long known to be widespread along the coasts of Europe, southward to the Irish Sea (Zimmer, 1909). And the fact that it was much more frequent in the northern sector in February and April (32% and 20% of the stations, respectively) than in May (8%), June (6%), July (8%), or in October when it was not taken at all, is evidence that its presence within our limits depends chiefly, if not wholly on immigration. The largest catch of Erythrops was 4 c.c., near Shinnecock on June 8, 1930.

AMPHIPODS

Euthemisto compressa

Until comparatively recently, it was generally accepted that the two named representatives of Euthemisto, that have long been known to abound off the northeastern coasts of the United States, *compressa* Goes, and *bispinosa* Boeck, were well defined species. Stephensen (1924, p. 103) has, however, shown from examination of extensive series from different parts of the Atlantic and Mediterranean that while typical specimens of the two are easily separable, intermediates occur so often that he has definitely classed them as "formae" of the one species *compressa*.

Frequency. The genus Euthemisto (treated here as a unit) rivals *Calanus finmarchicus* in frequency of occurrence, for it was taken at every station on eight of the cruises, and at 38% of the stations on all cruises combined, though it may be only irregularly represented on occasion, as in May and June 1929 (38% and 27% of the stations respectively). No preponderance is indicated either north or south, but slightly greater frequency is probably characteristic for it offshore (92%) than inshore (77%), which accords with what is known of its occurrence in the Gulf of Maine (Bigelow, 1926) and with previous records for the genus in the region now under consideration (Bigelow, 1915; 1922).

Relative monthly percentages perhaps warrant the generalization that Euthemisto tends in most years to be slightly less frequent in early or mid-summer, than in late winter or spring, it being especially suggestive that an alteration of this sort took place in 1930, for Euthemisto was universal in that year up to June. And sharper fluctuations may occur in other years, as illustrated by 1929, when the frequency decreased progressively by more than ½ from April through June, but then rose again by July to a level higher than had existed in April.

Abundance. With Euthemisto so nearly universal, throughout the area in most years, it is interesting to find the catches averaging only about 30 c.c., at most, in any month (May 1930), while the average for the whole area (all cruises combined) was only about 11 c.c. for the years 1930–1932, and 2.5 c.c. for 1929. Among 509 recorded catches of Euthemisto, only 26 were larger than 40 c.c., with a maximum of 320 c.c. at a station on the inner part of the shelf off Atlantic City, June 27, 1930.

The seasonal gradient in abundance has varied too widely from year to year for generalization as to the normal cycle, except that the catches averaged very small in February and in April, in each year. In two of the years (1931, 1932), the catches of Euthemisto continued to average small, right through the season in spite of an occasional rich catch, e.g., 63 c.c. at Station 21415, May 25, 1932. Considerable augmentation was, however, recorded in the other two years, culminating in June or July, as appears from the following tabulation:

Average volumes of Euthemisto

Month	Year	Inshore	Offshore	North	South	Area surveyed	Maximum
February	1930	2	1	1	1	2	9
	1931	3	3	1	.5	3	17
	1932	6	8	7	6	7	40
April	1929	<1	<1	<1	<1	<1	2
	1930	7	5	6	8	7	50
May	1929	<1	<1	<1	<1	<1	5
	1930	23	33	24	23	27	106
	1931	<1	<1	<1	<1	<1	<1
	1932	<1	<1	<1	<1	<1	63
June	1929	6	1	1	1	3	84
	1930	36	9	22	41	25	320
	1930	2	<1	<1	3	1	48
	1932	<1	6	<1	7	3	47
July	1929	4	2	2	5	3	19
	1930	37	3	27	—	27	94
	1931	1	4	1	—	1	27
October	1931	—	1	<1	3	1	15

Regional volumes also show that Euthemisto may average most abundant either inshore or offshore, or be about as abundant in the one belt as in the other, at any given time. But the inshore belt has most frequently been the more productive of the two on occasions when any significant inshore-offshore gradient has

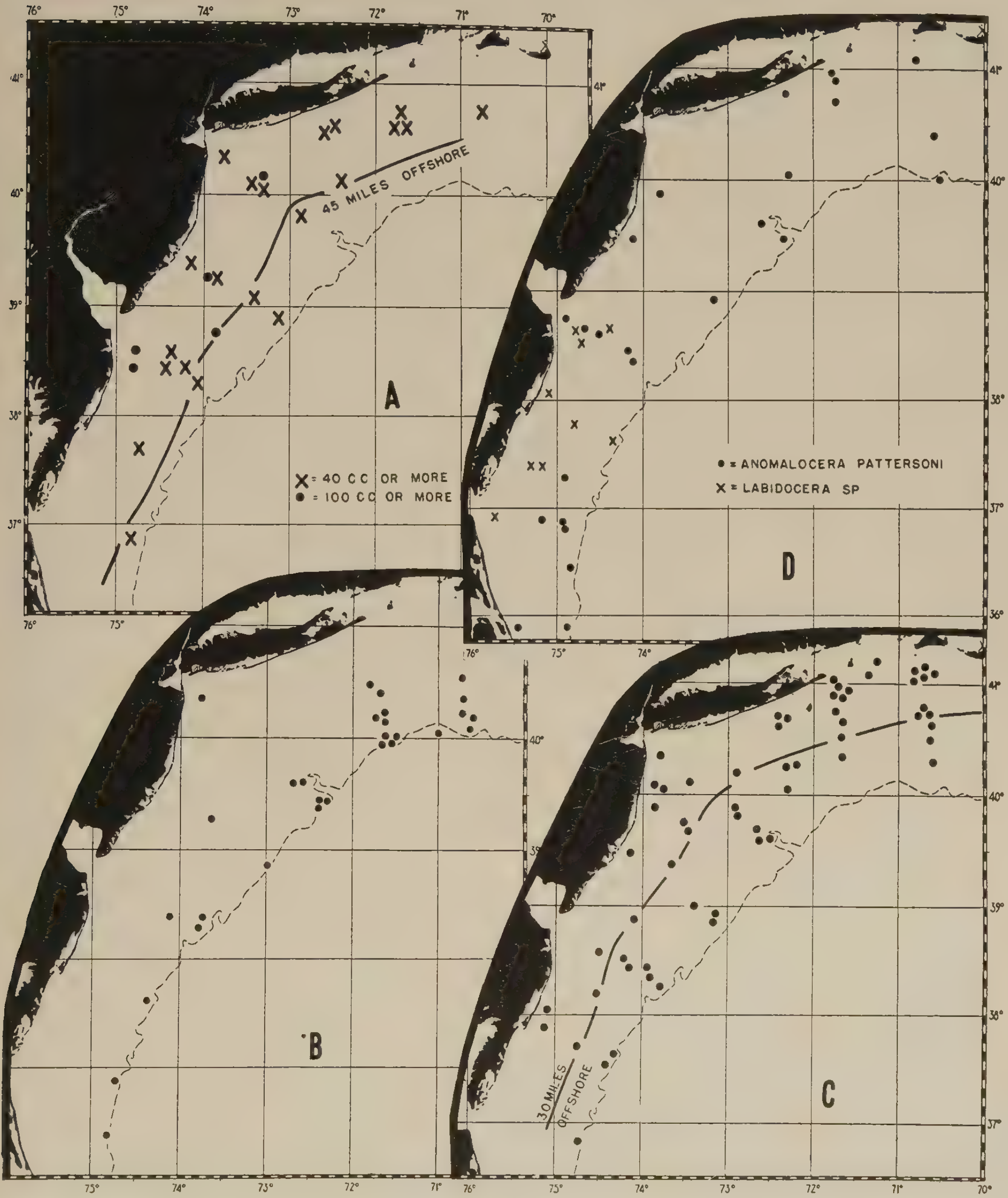

76°
75°
74°
73°
72°
71°
70°
41°
40°
39°
38°
37°
36°
45 MILES OFFSHORE
A
X = 40 CC OR MORE
● = 100 CC OR MORE
● = ANOMALOCERA PATTERSONI
X = LABIDOCERA SP
D
B
30 MILES OFFSHORE
C

Fig. 22. Locality records, all cruises combined: A, large volumes of *Euthemisto compressa;* B, Phronima; C, *Acartia longiremis,* inshore and offshore; D, *Anomalocera pattersoni* and Labidocera.

existed, resulting in a general average about twice as great there as offshore (Table, p. 300). And the few catches larger than 100 c.c., as well as the majority of those larger than 40 c.c. have all been within 45 miles of land (Fig. 22A), which contrasts sharply with conditions eastward from Cape Cod (Bigelow, 1926, p. 157, Fig. 55).

Euthemisto has averaged about equally abundant south as north, February-May, but considerably more so south than north, in June, on the three occasions when any significant gradient existed in this respect (Table, p. 300). But we have some evidence that the center of population tends to shift northward, as summer advances, in the fact that relatively large catches were recorded only in the most easterly sector of the area in July-August of 1913, and northward from the Cape May profile in the latter month of 1916 (Bigelow, 1915; 1922). A shift in this direction would, indeed, be the natural expectation for a boreal species, with the seasonal warming of the waters.

Conditions in October 1931 when Euthemisto averaged 3 c.c. in the southern sector, but less than 1 c.c. in the northern—if characteristic—suggest that the center of population again shifts southward, early in the autumn. And this is corroborated by the fact that rich catches were made near Delaware Bay and off Chesapeake Bay in November 1916 (Bigelow, 1922).

Annual variations. Little annual difference in the average volumes of Euthemisto has been recorded for February, April, or May. But in June and July, the catches averaged about 27 times as great in the richest year (1930, average, 27 c.c.) as in the poorest (1931, average, 1 c.c.), evidence that while the status of this species at the end of the winter and late spring is comparatively constant from year to year, very wide differences in this respect may develop in summer, even within a short series of years.

OTHER AMPHIPODS

Other than Euthemisto, and specimens of one gammarid or another picked up when the tows were made close to the bottom, the only amphipods detected in the catches were Phronima and Hyperia. The former has been recorded rather frequently offshore in the north, rather less so offshore in the south, and once close inshore off New York (Fig. 22B). The fact that Phronima was recorded at 2–5% of the stations from February to June, but at 15% in July and 13% in October suggests that this visitor from offshore is to be expected in on the shelf more often in midsummer and autumn than earlier in the year. The maximum catch (13 c.c.) was also made in July, all other records being based on occasional specimens only.

Hyperia was recorded at two stations—one in April 1930 off Currituck at the continental edge, the other at a similar locality off Atlantic City in June 1931.

COPEPODS

ACARTIA

In the Gulf of Maine, where *A. longiremis* is endemic and widespread, though never very abundant, it appears to be confined to the shoaler waters (including the offshore banks as well as the coastal zone) during the cold half of the year, to disperse out over the deep basin in spring, summer, or autumn, when its numbers increase (Bigelow, 1926, p. 180). And its distributional status is essentially the same to the west and south of Cape Cod, for while it is abundant in Chesapeake Bay throughout the year—most so, in fact, in March—(Wilson, 1932a, p. 20), we have only two records of it out on the shelf in February and one in April, whereas in May, June, and July, it was found about as frequently offshore (7% of the stations) as inshore (9%), for the several years combined (Fig. 22C), and at 20% of the offshore stations during the only October of record.

The records of occurrence do not suggest any regularly latitudinal gradient during the season of its offshore dispersal, between the offings of Martha's Vineyard and of Delaware Bay. But it was taken at one station, only, south of the Winterquarter profile, a failure in the extreme south that is difficult to explain in the face of its constant and abundant occurrence in Chesapeake Bay at the same times of year.

Within Chesapeake Bay and probably in other similar situations along our mid-Atlantic coast, *A. longiremis* ranks second only in abundance to *A. clausii* among the copepod fauna (Wilson, 1932a). Out over the continental shelf, however, our maximum catch was at the rate of but 16 c.c., while 11 only out of the 60 odd catches were as voluminous as 5 c.c. However, the fact that about 1/3 of the catches were 1 c.c. or larger, shows that a sufficient population of it exists (and widespread) in the shelf waters for local concentrations to be expected (though not actually encountered as yet) should a happy combination of circumstances favor its reproduction.

A. clausii is described by Wilson (1932a) as the chief copepod constituent of the plankton in Chesapeake Bay. We have but one record of it, however, out on the shelf, evidence that it is far more strictly neritic within our limits than in the Gulf of Maine, where it is widespread, inshore and offshore alike, and may constitute even up to 30–50% of the copepods by number locally, in the coastwise belt, at the season when it is most plentiful (Bigelow, 1926, Fig. 59).

A. tonsa—probably an indicator of coast water—swarmed at three stations near the mouth of Delaware Bay, in August 1916; otherwise, we have no record of it within our limits, nor did Wilson (1932a) report it from Chesapeake Bay, though it is a dominant species inshore, and in brackish situations near Woods Hole in summer (Fish, 1925; Sharpe, 1910; Sumner, Osborne, and Cole, 1913).

Anomalocera pattersoni

The "blue copepod," widespread, though never very abundant, in the Gulf of Maine (Bigelow, 1926, Fig. 63) had already been reported in summer at various localities along the continental shelf to the offing of Chesapeake Bay, inshore and offshore alike (Bigelow, 1915, Fig. 69). And the records for the period 1929–1932 corroborate this distributional picture, being generally distributed across the shelf, from the northern boundary of our area to the southern (Fig. 22D). It seems, however, that Anomalocera is considerably less frequent—though so widespread—to the west and south of Cape Cod than it is over George's Bank and in the Gulf of Maine, for it was detected at about 4% only of the stations for the series as a whole. And being so conspicuous an object, even after its beautiful blue color has faded in the preservative, it is not likely that any of its adults were overlooked.

It is questionable, with so few data, whether the monthly distribution of catches (2% of the stations for February, 7% for April, 4–5% for May and June, and 12% for July) indicates any regularly seasonal cycle between late winter and midsummer. But failure to take it at all during the one October cruise may perhaps reflect autumnal impoverishment.

We have no reason to suppose that Anomalocera is ever of volumetric importance in the waters under study, except on rare occasions, for while one catch was at the rate of 32 c.c. (near Cape May, June 1930), most of the other records for it were based on occasional specimens only.

Calanus finmarchicus

Frequency. In February, when (by present indications) Calanus is close to its lowest ebb for the year, it occurred generally throughout the area southward to Latitude 36°, both in 1930 and in 1931; southward, in fact, beyond Cape Hatteras in the latter year. But it was recorded at 38% only, of the stations inshore, in the southern sector, in the abnormally warm February of 1932, though it was universal then in the north, and almost equally so along the offshore belt in the south (90% of the stations).

If the data for April, of 1929 and of 1930, be representative of the normal mid-spring state, it appears (as might be expected) that Calanus tends by that month to populate any restricted areas where it may have been absent at the end of the winter. And it has either proved universal (100% of the stations), throughout the area as a whole from April or May through June, as was the case in 1930 and 1931, or has at most been lacking at scattered stations, here and there, as in 1929 and 1932:

Percentage of stations with Calanus, for the area as a whole

Month	1929	1930	1931	1932
February	—	77%	100%	56%
April	100	95	—	—
May	100	100	100	95
June	91	100	100	97
July	91	100	100	—

Calanus has proved equally universal every year in July, in the sector eastward from the offing of New York. But wide differences in this respect are evidently to be expected from year to year in the southern sector, at that season, for while it was universal there also, in the summers of 1916[1] and of 1929, record of it south of New York in July 1913 was confined to a few scattered stations. Clarke and Zinn (1937) found it regularly through August and September near Martha's Vineyard. And it continues universal over our area as a whole through the autumn (at least in the years when it is widespread and abundant in summer) for it was recorded at 12 out of 13 stations along the offshore belt, north and south, in October 1931, and at every station in November 1916. Conditions in February (p. 304) suggest that at least a sparse population of Calanus persists throughout the area as a whole, over the winter in most years, as is certainly the case near Martha's Vineyard in the northeast (Clarke and Zinn, 1937). But our records do not show how early, in autumn, Calanus may repopulate the southern sector, after a summer when it is scarce or absent there, nor at what season it becomes scarce there, in a year (e.g., 1932) when winter cooling does not proceed to the usual extreme.

Abundance. Clarke and Zinn (1937) report Calanus as at its minimum, near Martha's Vineyard, during the autumn and winter, and this applies over our area as a whole, with an average volume of only about 14 c.c. for February 1930, 1931, and 1932 combined (Table, p. 309).

The most interesting event in the seasonal cycle of this copepod is that it greatly increases in abundance at some time during the spring. Unfortunately, data for March are confined to the immediate vicinity of Martha's Vineyard (Clarke and Zinn, 1937), where Calanus was still as scarce in that month as in February. But the catches (for the area as a whole) averaged 18 times as great in April as in the preceding February in the one year (1930), when surveys were made in both these months, and 29 times, 9 times, and 10 times as great in May as in February of 1930, of 1931, and of 1932, respectively (Table, p. 309). Average volumes for successive months suggest that following this vernal augmentation, Calanus in the north may either decrease after April, as in 1929, or may continue at a roughly constant level of abundance through May, June, and July, as in 1930 and 1931[1] After an unusually tardy spring—as in 1916—Calanus may, in fact, continue in great abundance through August (Bigelow, 1922), even in the southern sector. But in other years, illustrated by 1929, Calanus markedly decreases in the south, through late spring and early summer; or in a warm summer—by the evidence of 1913—it may practically disappear thence by July. We should, however, caution the reader that description of the seasonal trend in terms as general as the foregoing applies only if regional and short term irregularities be smoothed out by the process of averaging, and that some such succession of peaks and valleys, as appears in Clarke and Zinn's (1937, Fig. 4) graph of seasonal abundance near Martha's Vineyard, would more correctly picture the conditions to be expected at any given station.

---

[1] Reexamination of samples, from the July-August cruise of 1916 has revealed the presence of at least a few Calanus at every station.

Data for early autumn are confined to the vicinity of Martha's Vineyard, where Clarke and Zinn (1937) record a sharp decline in the abundance of Calanus from July through August, with only trifling numbers in September, or later in the autumn. And this probably applies over our area generally, judging from the facts that average and maximum values had fallen, by October, about back to those existing in the preceding February, in the one year (1931), when surveys were made in both these months, and that Calanus also greatly decreased in abundance between July-August and November in 1916 (Bigelow, 1922). But the data fail to show whether it is characteristic for this autumnal impoverishment to follow after the spring or summer as abruptly, in other parts of our area, as it does in the extreme northeast, as illustrated by Clarke and Zinn's station, nor is any information available for December or January, elsewhere within our limits.

No rich centers for this species yet exist in February, nor do the average volumes (Table, p. 309) suggest any definite gradient, either north-south, or inshore-offshore, as generally characteristic at this time of year, at least down to Latitude, about 36° N., south of which Calanus was negligible quantitatively in the one year of record (1931). In normal years, the vernal augmentation of Calanus is, however, accompanied by a localization of the chief centers of abundance within the sector bounded by the Montauk and Cape May profiles —such, at least, was the case in 1929, and again in 1930 (Fig. 23). And while the data for April do not indicate any more likelihood of greatest abundance in any one locality than in another within these boundaries, the center of abundance yearly becomes still more definitely concentrated by May within the area outlined in Fig. 23A. This alteration involves, on the one hand, a contraction seaward of the inshore margin of the productive area in the south, and on the other hand, its expansion eastward, at least as far as the Martha's Vineyard profile.

---

[1] July data for 1930 and 1931 were limited to the northern sector.

In normal summers (e.g., 1929, 1930, 1931), the situation in this respect, is much the same in June, and in July as it is in May. But after a cold and tardy spring (e.g., 1916), rich concentrations of Calanus may also persist along the outer belt of the shelf as far south as the offing of Chesapeake Bay, until well into August. Hence, (presumably) in a year of this type, vernal augmentation on a large scale, is not as definitely centered in the northern sector, as usual. Even in 1916, however, the largest catches of all[1] were to the northward of the Cape May profile, while catches of more than 800 c.c. for May, June, and July of all years combined (Fig. 23), have been so definitely concentrated, offshore, in the sector north and east of the Atlantic City profile, that this may well be named the "Calanus" belt. Here, the average volume for these months has been 252 c.c. (65 c.c., in 1932; 339 c.c. in 1929–1931), the maximum 1556 c.c., the minimum 0 c.c.

In the easternmost sector, east of Longitude about 73° W., the area of abundance may or may not reach shoreward within 5–10 miles of the coast, in late spring or summer. But the facts that our largest catch at any one of the three June-July stations near Block Island was only 583 c.c., with 10–33 c.c. at the other two, and that the maximum reported near Martha's Vineyard by Clarke and Zinn (1937) corresponds to less than 90 c.c. when reduced to our present standard, makes it unlikely that dense aggregations of Calanus ever occur close in to this part of the shore line, even at the season of peak abundance. And this

---

[1] Bigelow, 1922, 3000 c.c. or more per haul.

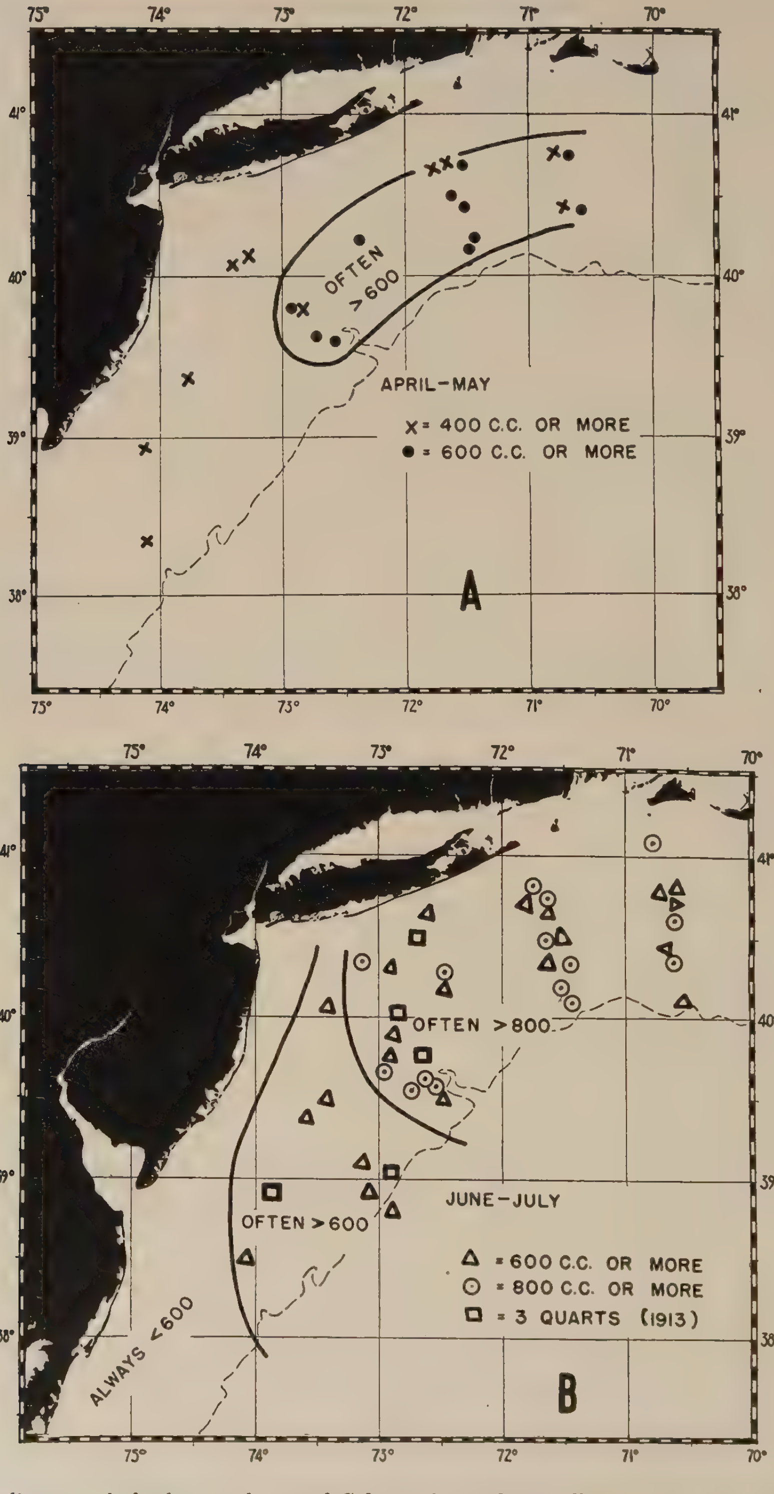

75°
74°
73°
72°
71°
70°
41°
40°
39°
38°
OFTEN >600
APRIL–MAY
X = 400 C.C. OR MORE
● = 600 C.C. OR MORE
A
OFTEN >800
OFTEN >600
ALWAYS <600
JUNE–JULY
△ = 600 C.C. OR MORE
⊙ = 800 C.C. OR MORE
□ = 3 QUARTS (1913)
B

Fig. 23. Locality records for large volumes of *Calanus finmarchicus*, all cruises combined: A, April and May; B, June and July.

inshore belt of summer scarcity, some 20 miles wide off New York, expands seaward toward the south in normal years until it includes the entire breadth of the shelf off Winterquarter, as outlined in Fig. 23B. Neither have large volumes ever been recorded farther seaward than the 200-meter contour.

Data as to chief centers of abundance are lacking for September. But the situations existing in October 1931 and in November 1916 (Bigelow, 1922), make it unlikely that any areas, describable as "rich" by spring or autumn standards, characteristically exist anywhere westward or southward from the offing of Martha's Vineyard in normal years, at any time from late summer, through autumn or winter.

Average volumes of *Calanus finmarchicus*

Month	Year	Inshore	Offshore	North	South	Area surveyed	Maximum	Minimum
February	1930	9	5	11	3	7	24	0
	1931	29	30	6	32	29	117	<1
	1932	7	1	7	4	5	43	0
April	1929	115	256	228	128	173	1532	<1
	1930	129	119	172	71	121	852	0
May	1929	51	152	136	35	91	435	<1
	1930	163	260	259	138	206	1063	<1
	1931	117	429	309	105	251	1514	<1
	1932	22	106	60	33	50	407	0
June	1929	44	135	109	29	81	411	0
	1930	176	228	240	40	197	694	<1
	1931	301	578	497	237	406	950	<1
	1932	19	79	42	48	42	228	0
July	1929	81	68	99	18	75	377	0
	1930	281	236	254	—	254	856	<1
	1931	402	589	473	—	473	1274	<1
October	1931	—	17	18	15	17	62	0

Average volumes of *C. finmarchicus*, all years combined

Month	North	South	Inshore	Offshore
February	8	13	15	12
April	196	99	109	189
May	191	78	88	234
June	222	93	134	255
July	255	18[1]	298	275
October[2]	18	15	—	17

[1] 1929 only.

[2] 1931 only.

Breeding periods. It seems reasonably established, from the brevity of the annual period of abundance, that there is only one major breeding period for Calanus in the waters southward from the New York profile. Clarke and Zinn's (1937) analysis of relative percentages of different stages pointed, however, to two shorter-lived generations during the spring, followed by a longer lived one in summer in the northeastern sector of our area. The offshore catches throw no light on this point, for the younger stages were not adequately sampled.

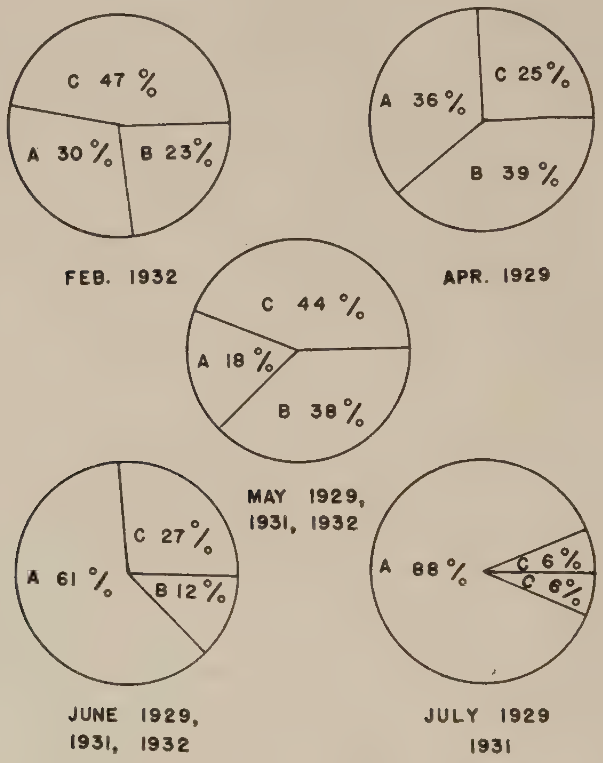


Fig. 24. *Calanus finmarchicus*: percentage of cases, in different months, where the deep catch was twice as large was the shoal (A); the shoal catch twice as large as the deep (B); and neither catch twice as large as the other (C).

But whether separate generations can be distinguished or not, the volumetric succession from month to month is sufficient evidence that effective reproduction is confined to spring and early summer, north as well as south.

Vertical distribution. In February (1932), April (1929), and May (1929, 1931, 1932) combined, the shoal catch was about as large as the deep (ratio, less than 1 to 2) at about one-fourth to one-half the stations where hauls were made at two or more levels, and significantly the larger as often as the reverse among the remaining cases (Fig. 24). The deeper catch was, however, at least twice the more voluminous in about 61% of the cases in June, and in about 88% in July, with only about 6% of the cases failing to show definite stratification of the one order or the other in the latter month (Fig. 24). The volumes of Calanus for all pertinent stations combined also averaged about 2–6 times as great at 20–40 meters as at 10–0 meters in February, April, and May, more than 25 times as large in June and about 400 times as large in July, as follows:

Average volumes of *C. finmarchicus* at deeper levels relative to those at 10–0 meters

Month	Year	20–40 Meters	No. of Cases	More than 40 Meters	No. of Cases
February	1932	2.6	11	1.3	7
April	1929	5.8	8[1]	2.3	12
May	1929 1931 1932	4.4	92	0.8	18
June	1929 1931 1932	23.5	80	8.2	14
July	1929 1931	399.2	28	105.8	13

[1] Omitting one case, where the deep catch was 135 times as great as the shoal.

And the vertical distribution of rich (> 300 c.c.) catches has shown a corresponding transition from June to July:

Frequency of large volumes (> 300 c.c.) at deeper levels relative to the upper 10 meters

	20–40 M.	<40 M.
February, 1932	—	—
April, 1929	1.8 to 1	0.8 to 1
May 1929, 1931, 1932	1.8 to 1	1.4 to 1
June 1929, 1931, 1932	6.2 to 1	4.3 to 1
July 1929, 1931	29.0 to 1	12.5 to 1

These depth relationships may be summarized as follows: In late winter and through the spring, the richest population of Calanus is close to the surface about as often as in mid-depths, but the stock averages somewhat more voluminous in the 20–40 meter stratum, than in the superficial 10 meters of water, even at this season. Rather an abrupt transition then takes place between May and June, to the summer state, in which Calanus is definitely concentrated at depths of 20 meters or more, and this vertical gradient is greatly accentuated from June to July. But it is not until the latter month that the stock living deeper than about 40 meters shows any great increase in abundance relative to that near the surface.

Diurnal migration. Successive hauls, day and night, were made at one station only, near Fire Island on May 17, 1929. And it is questionable how these should be interpreted, as regards Calanus—for while a disappearance of Calanus from the immediate surface, during the interval between 3 A.M. and 11 A.M., followed by reappearance in abundance there between 11 A.M. and 6 P.M. is compatible with diurnal migration, obviously this can not explain the subsequent decrease in the ratio of surface catch to deep catch between 6 P.M. and 11 P.M., nor the progressive increase in the average abundance of this copepod for the water column as a whole that took place during the period over which the observations were extended (Fig. 25). We are, therefore, forced to turn to a comparison of deep catches with shoal, from station to station, for information as to the extent to which diurnal migration affects the mass distribution of Calanus. Such a comparison shows that the deeper catch was significantly the larger of the pair about 1.3 times as often by day as by night as tabulated below, but that the

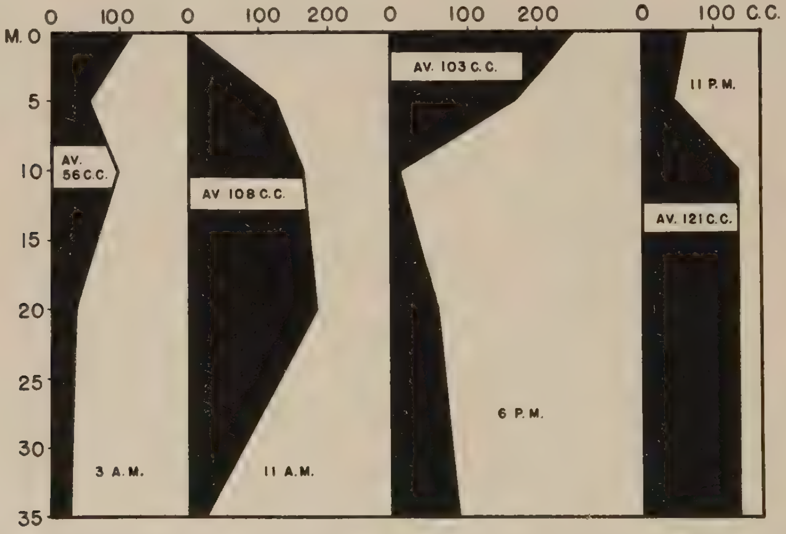


Fig. 25. Vertical distribution of Calanus, near Fire Island, May 17, 1929, at 3:00 a.m., 11:00 a.m., 6:00 p.m. and 11:00 p.m.

shoaler was the larger about 1.4 times as often by night as by day, for the months February-June, as a whole. And while a contrast of the reverse order prevailed in July, the number of night hauls for that month was so small (12) that it may not be significant.

Percentage of cases in which the shoal catch was twice as great as the deep (A), the deep catch twice as great as the shoal (B), and neither one twice as great as the other (C), by day and by night.

	Day				Night			
	A	B	C	Cases	A	B	C	Cases
February, 1932	17%	17%	67%	6%	20%	30%	50%	10%
April, 1929	18	45	36	11	25	17	58	12
Average — February-April	17	31	52	17	23	24	54	22
May, 1929, 1931, 1932	26	37	37	38	38	21	40	47
June 1929, 1931, 1932	8	70	23	40	10	61	29	49
July 1929, 1931	10	80	10	20	8	92	0	12

The volumetric ratio of deep catch to shoal, similarly, averaged about 5 times as great by day as by night for February, April, and May combined, about 1.5 times as great by day as by night for June, and about 2.2 times as great by day as by night for July, details for individual cruises being as follows:

Volumetric ratio, deep catch to shoal

	8 A.M.–4 P.M.		8 P.M.–4 A.M.	
	Ratio, all Stas.	Cases	Ratio, all Stas.	Cases
February, 1932	3.3 to 1	6	10.0 to 1	10
April, 1929	30.4 to 1	11	1.0 to 1	13
May, 1929	14.5 to 1	11	0.9 to 1	13
May, 1931	20.7 to 1	9	0.6 to 1	7
May, 1932	4.5 to 1	17	2.0 to 1	27
June, 1929	2.4 to 1	14	7.0 to 1	16
June, 1931	35.7 to 1	12	8.8 to 1	11
June, 1932	35.0 to 1	14	34.0 to 1	22
July, 1929	159.0 to 1	16	75.7 to 1	7
July, 1931	311.9 to 1	4	136.2 to 1	5

If we omit from the calculation the one station for each cruise where the ratio of deep volume to shoal was largest, thus minimizing the effects of occasional cases of very strong stratification, we find this ratio averaging 2–4 times as great by day as by night, and with no outstanding alteration in this respect between spring and summer, as follows:

Volumetric ratio, deep catch to shoal

	8 A.M.–4 P.M.		8 P.M.–4 A.M.	
	Ratio	Cases	Ratio	Cases
February 1932, April 1929, May 1929, 1932, 1932	3.8 to 1	50	0.9 to 1	65
June 1929, 1931, 1932	11.7 to 1	37	6.0 to 1	46
July 1929, 1931	124.1 to 1	18	35.5 to 1	10

A prevailing tendency toward diurnal migration on the part of adult Calanus, upward toward (or even to) the surface during the hours of darkness, and downward again by day, and on a scale sufficient to cause widespread alterations of similar order in the vertical distribution of the stock seems the only plausible explanation for the relationship just brought out. And it is especially interesting to find the evidence of this hardly less clear for July, when the temperature of the upper 10 meters has risen above the optimum for Calanus, than it is for June or for May, when the entire water column is of a temperature suitable for this copepod.

It is equally clear, however, that the effects on the distribution of Calanus of this tendency toward vertical migration varies widely from time to time and from place to place, for it has frequently happened that the shoal catch has been the greater even by day, and still more often that neither haul was much more productive than the other, irrespective of the time of day. But our data are not sufficiently detailed to show whether irregularities of these sorts result from differences in the degree to which different individuals respond to the effective stimulus (light), or from mass movements of the water, with its contained plankton.

Distribution in relation to temperature. In the summer of 1916, the most abundant stock of Calanus was living at depths and in the belt where temperature was lower than about 7° (Bigelow, 1922). And the catches larger than about 400 c.c., on our recent cruises have all been made at times and localities where the bottom stratum was at least as cold as about 8°, i.e., where a reservoir of cool water was not more than about 50 meters distant, even though the Calanus may have been close to the surface, and in much higher temperatures, at the time of capture. The boundaries of the "Calanus zone" for June and July (Fig. 23B) also correspond closely to those of the pool of cold bottom water characteristic of the mid- and outer part of the shelf, to the eastward of the Barnegat profile, at that season. Clarke and Zinn (1937) found, it is true, that Calanus was most numerous near Martha's Vineyard during July and August, when the bottom water averaged about 13°, but their maximum catches were at the rate of less than 90 c.c., when reduced to our standards, contrasted with the many catches larger than 1000 c.c. that were made closer to cold water on the "Albatross" cruises. And the relationship between average catch and temperature, for the several cruises on which hauls were made at two or more levels (Fig. 26), suggests that the lowest temperatures persisting on the shelf in summer (usually 6–10°) support, on the average, considerably the densest population of Calanus, and that the temperature range between 12° and 16° also may be classed as at least moderately favorable, with no apparent gradient within these limits. But Cala-

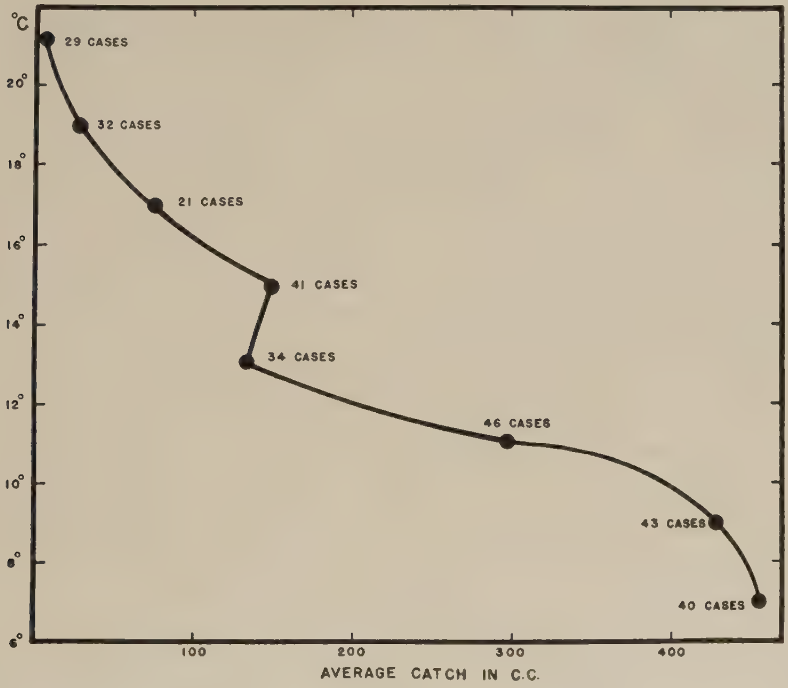


Fig. 26. Average catch of Calanus in water of different temperatures, irrespective of depth.

nus is much less abundant at higher temperatures, largely deserting the surface stratum whenever and wherever the latter warms above 18°, and practically disappearing thence (probably by sinking), whenever the temperature rises above 19–20°. In fact, 24 out of a total of 43 hauls centering in water of 19° or warmer, proved absolutely barren of Calanus, while each of 10 others yielded not more than 1 c.c., of the sizes large enough to be sampled by our nets. And while exceptions occur to this as to every other "rule" regarding the distribution of plankton,[1] we seem justified in concluding that the warming of the water column from above is the chief (if not the only) factor responsible for the progressive intensification of the vertical volumetric gradient for this copepod from May through June to July. Light, we may note in passing, seems ruled out as the control in this case, by the fact that stratification of Calanus is much more pronounced in July than in May, though the intensity of illumination is about the same in the one month as in the other.

Annual fluctuations. The tabulation of average volumes (p. 309) makes it clear that the stock of Calanus varies widely in strength from year to year, not only near the southern margin of its range (where this might be expected), but equally in the more northern sector where the species usually has its center of abundance. The average catch was in fact about 4 times as great in the most productive year (1931) as in the poorest (1932) for February, 5 times as great for May, 9 times as great for June, and at least 6 times as great for July. And while the comparatively small volumes prevailing in 1932 perhaps approximate the lowest level to which Calanus is likely to fall in our area, it may not be unusual for it to exist in considerably greater volume than in 1931, for such seems to have been the case in the summer of 1916, when swarms were encountered (Bigelow, 1922, p. 143).

The record also suggests that when Calanus is relatively abundant at the end of winter (e.g., 1931), it is likely to maintain preeminence in this respect through the spring and summer, but that a year that is poor in Calanus in February may either continue poor through spring and early summer, as happened in 1932, or may experience an active vernal multiplication of this copepod as in 1930.

Comparison of the average catch, with temperature, for different years, leads to the rather astonishing conclusion that the rate of vernal augmentation is affected only indirectly by the thermal factor, if at all, for the year (1932) when production was poorest was not abnormally warm at the end of the spring or in early summer, though it had been so in February. It is a question for the future, whether a very warm winter in this part of the sea ordinarily presages a poor production of Calanus during the ensuing spring.

---

[1] The following productive catches were made in hauls centering in the upper 10 meters in water warmer than 18°: 150 c.c., 20.2°, Shinnecock II, July 1931; 166 c.c., 18.9°, Martha's Vineyard I, July 1929; 163 c.c., 18.2°, Cape May IV, June 1932; and 113 c.c., 18.1°, New York IV, June 1932.

CALANUS HYPERBOREUS

Calanus hyperboreus[1] was taken at one station, only, in February, and was either absent altogether in April (1930) or was so scarce then that it was not detected. But it has appeared in one part of the area or another in May in each year of record with sufficient regularity to suggest that this is an annual event.

In 1930, for example, a year when a considerable indraft of cold water took place into the most eastern sector sometime in February or early March (Bigelow, 1933, p. 30), *C. hyperboreus* was generally distributed over the entire area by the middle of May right down to the offing of Chesapeake Bay (Fig. 27), locally in some abundance (up to 40–50 c.c.). It was similarly widespread east of the New York profile in that month of 1931, though chiefly confined to the outer part of the shelf farther south, which corresponds to the fact that little cold water had drifted past Nantucket in that year. And the first half of May again saw it at several stations in the eastern and mid-sectors, in 1932, and even off Chesapeake Bay where one haul yielded 23 c.c., seemingly following the indraft from the east that had taken place earlier (Bigelow, 1933, p. 30), though its presence was so short-lived that it was not found at all in the third week of the month.

In some years repeated invasions may also occur, as in 1932, when *hyperboreus* reappeared in small numbers, at the end of May, along a tongue extending from the outer part of the shelf off Martha's Vineyard and New York, westward to the offing of Atlantic City (Fig. 27), following a second invasion of cold water that had passed the offing of New York, two weeks or so before (Bigelow, 1933, p. 30). But in other years (e.g., 1930 and 1931), there may be only one invasion,—sometime perhaps none at all. In any case, we have no evidence that such events normally happen later than the end of May, for our records for *hyperboreus* in summer and autumn are confined to one station in July 1931, two in June 1932, and one in August 1916, off Martha's Vineyard, off Montauk, off New York, and off Delaware Bay respectively.

The evidence is thus conclusive that *C. hyperboreus* is not an endemic inhabitant of our area, but that it may be expected to appear here and there in late spring, after indrafts of water from the east, which accords with previous knowledge that it is widespread throughout the Gulf of Maine at that season, at least in some years, as well as on George's Bank (Bigelow, 1926, Fig. 68, 69, Fish and Johnson, 1937). It also seems certain—from the brevity of the periods during which *C. hyperboreus* has been present in our waters—that the effects of each wave of immigration endure only for the lives of the individual concerned, i.e., that this species does not reproduce successfully anywhere west of Nantucket.

---

[1] No regular record was kept of the presence or absence of this species in 1929.

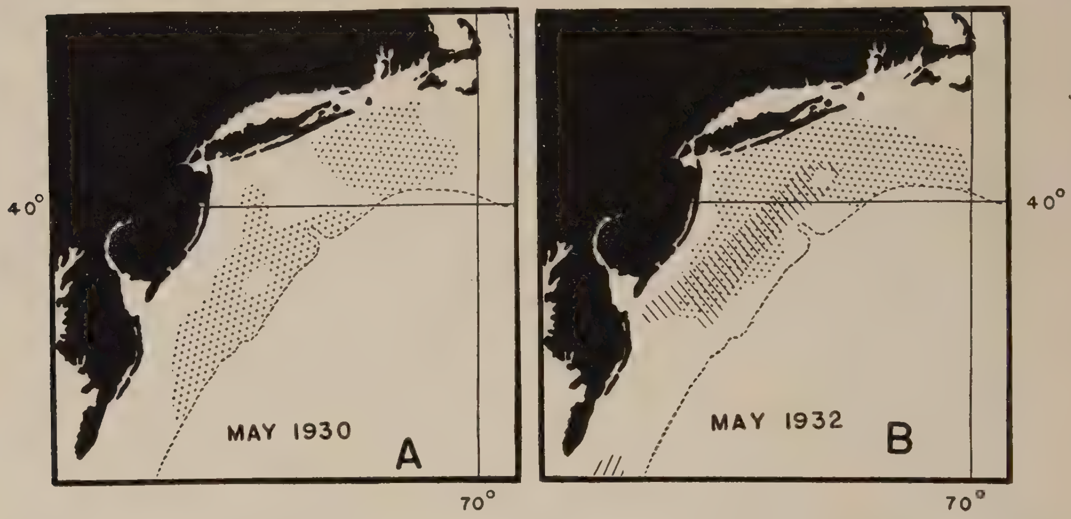


Fig. 27. Areas of occurrence of *Calanus hyperboreus:* A, May 12–23, 1930; B, May 2–6 (dotted), and May 9–16 (hatched), 1932.

C. hyperboreus is both so large and so easily recognized that it is perhaps the most reliable indicator-species for water from this source in our area. It is, however, negligible from the volumetric standpoint, except for brief periods, and of minor importance even then, witness a maximum catch of only 62 c.c. and an average of 25 c.c. within its area of occurrence in the month (May 1930) when it was taken most frequently and in greatest abundance.

Candacia armata

Previous records of this widely distributed copepod within our area were confined to the extreme south, where it was found in some abundance near the outer edge of the continental shelf and over the continental slope in the summers of 1913 and 1920, as well as in Chesapeake Bay on one occasion (Bigelow, 1915; Wilson, 1932a). But it was also to be expected in the north, having been found in the Gulf of Maine, as well as off the seaward slope of the latter (Bigelow, 1926, p. 219; Fish and Johnson, 1937, Fig. 25). And the records for 1929–1932 (Fig. 28) show that it does in fact occur about as generally as does *Euchirella rostrata*, throughout the offshore belt of our area (40% of the stations) and not rarely inshore as well (13% of the stations). It has also proved about as frequent relatively, north (27% of the stations) as south (21%). The monthly percentage of stations at which Candacia was taken in the offshore belt (16–17%, February-April; 40–54%, May-July; 60%, October), show it as entering our boundaries

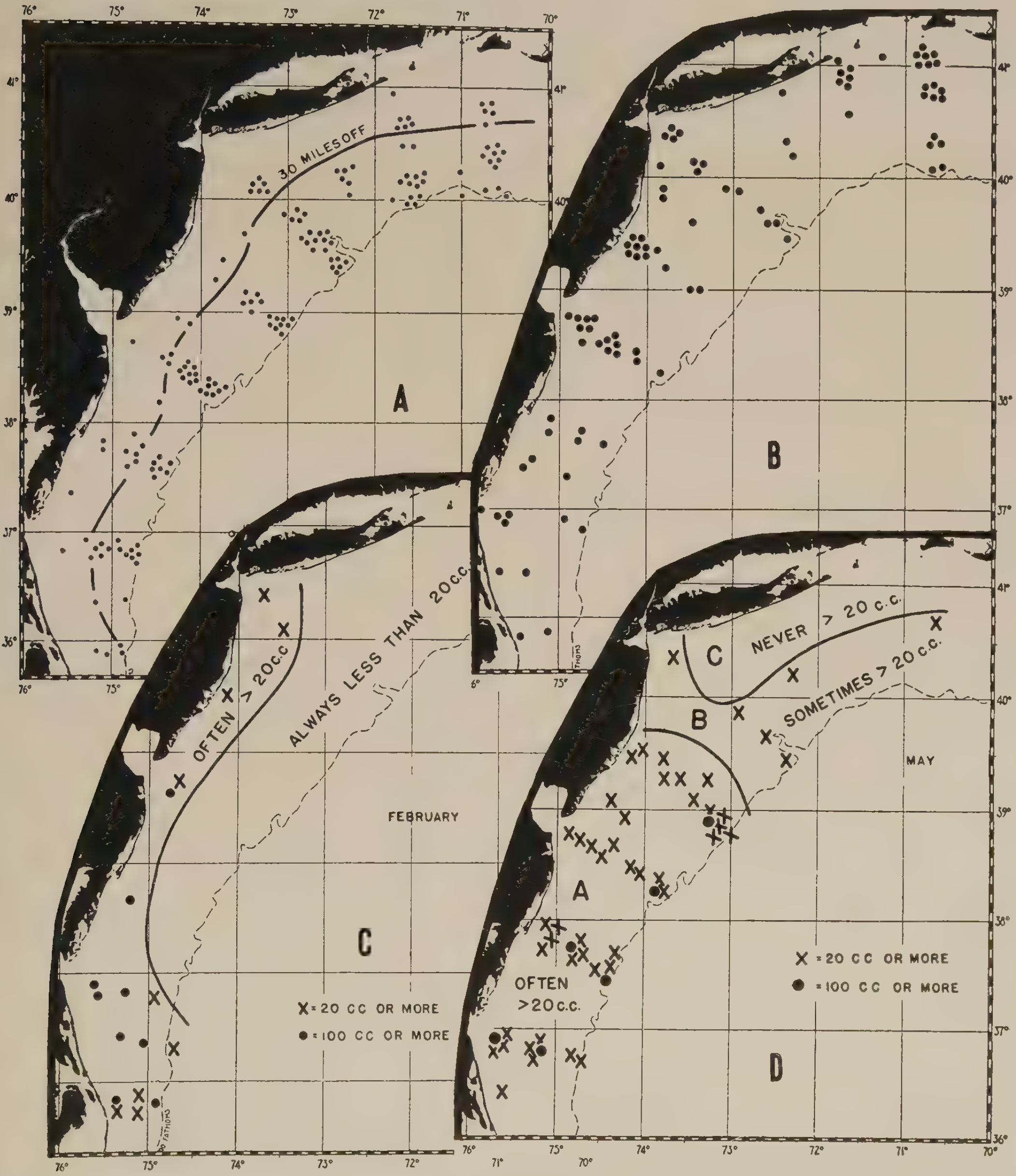

A
30 MILES OFF
B
C
OFTEN > 20 C.C
ALWAYS LESS THAN 20 C.C.
FEBRUARY
X = 20 CC OR MORE
● = 100 CC OR MORE
D
NEVER > 20 C.C.
SOMETIMES > 20 C.C.
MAY
OFTEN >20 C.C.
X = 20 CC OR MORE
● = 100 CC OR MORE
76° 75° 74° 73° 72° 71° 70°
41° 40° 39° 38° 37° 36°

Fig. 28. Locality records, all cruises combined: A, *Candacia armata*, offshore and inshore; B, *Centropages hamatus;* C, *Centropages typicus*, large volumes, in February; D, *C. typicus*, large volumes in May.

much more often from late spring through the summer, than in late winter or early spring, and perhaps somewhat more often still, in the autumn, while the maximum catch of 113 c.c. was also made in October. But we have no evidence that this seasonal invasion extends to the inshore belt, where on the contrary, it proved about as frequent in February and April (19%, 10% of the stations) as in May, June, or July (14%, 13%, 10%), a regional difference associated no doubt with prevailing drifts.

In 132 out of the 154 cases, the catches were of stray specimens. A catch of 113 c.c. was, however, made midway of the shelf off Cape May on October 23, 1931, evidence that Candacia may occasionally occur in abundance over restricted areas in autumn, suggesting local centers of reproduction. But we have no evidence that this ever happens earlier in the season, for five only of the other catches were larger than 10 c.c., with 16 c.c. as the maximum for this group.

Centropages hamatus

This copepod, generally considered as of more definitely boreal habit than its relative, *C. typicus*, and common in the Gulf of Maine, had previously been reported as far south as the offing of Chesapeake Bay as well as within the latter (Wilson, 1932a). The records for the years, 1929–1932, show, in fact, that its range actually extends southward past the offing of Chesapeake Bay nearly to Cape Hatteras (Fig. 28), in early spring. But while Wilson (1932a) reports it off Chesapeake Bay in August, we have no records of it south of Delaware Bay as late as July either of 1929 or of 1913, suggesting that it tends to disappear from the southernmost sector by midsummer in normally warm years.

It is also interesting to find that the records of occurrence of *C. hamatus*—though most frequent inshore—extend across the whole breadth of the continental shelf, from the northern end of our area to the southern, in one month or another (Fig. 28B), whereas in the Gulf of Maine, this copepod is chiefly confined to the close vicinity of the coast (Bigelow, 1926, Fig. 70). The monthly distribution of catches (12–13% of the stations for February and April, 16% for May, 19% for June, and 10% for July), indicates a general tendency for this species to increase somewhat in frequency from late winter to June, and then to decrease somewhat later in the summer. And the data for the one October of record point to a still farther decline in the autumn, for it was not recorded at all on that cruise, nor in November 1916.

On rare occasions, a rich stock of *C. hamatus* may develop locally in the northern sector, suggesting active reproduction, cases in point being 189 c.c., near Martha's Vineyard, June 1930; 59 c.c. at that same locality on May 19, 1932; and 35 c.c., close in to Chesapeake Bay, in April, 1929. Other than these, however, the largest catches were 10–16 c.c. (5 cases), the average for the whole series being about 4 c.c. at the stations where *C. hamatus* occurred, and less than 1 c.c., if the stations where it failed be included in the calculation. Neither did *C. hamatus* form as much as 1% in any subdivision of the area during any cruise.

CENTROPAGES TYPICUS

Frequency. *Centropages typicus* is but little less omnipresent than *Calanus finmarchicus* (p. 304) throughout the whole area, from north to south, and out to the 200-meter contour,—recorded, in fact, at about 90% of the stations, for all months and years combined—, and it is possible that young stages of the species may have been actually present, even at the few localities where the catches failed to show its presence.

Percent of stations with *Centropages typicus*

Year	February	April	May	June	July	October
1913	—	—	—	—	63%	—
1929	—	100%	95%	—	91	—
1930	86%	100	93	61%	94	—
1931	86	—	80	65	71	100%
1932	76	—	98	100	—	—
Aver.	82	100	94	77	85	—

The percentages of the stations where *C. typicus* was recorded suggest some increase as characteristic from February to April, succeeded in some years by some decline in summer, but then by recovery by October. In some years (e.g., 1932), however, this copepod may be as universal in June as in April.

Abundance. In the northern sector, the average stock of *C. typicus* is at its lowest ebb at the end of winter, and continues relatively low through spring and early summer, when an average of less than 15 c.c. is to be expected in normal years, but increases some 4–30 fold (to 90–100 c.c.) by July. Clarke and Zinn's (1937) records further show that *C. typicus* may continue numerous through August, in the easternmost sector of our area, with abundant production of young, and—by the evidence of the single year, 1931—it may be expected to remain at about the same high level until mid-autumn.

The seasonal cycle is much less regular in the south, where the average volume remained at a comparatively constant level from early spring through midsummer in one year (1929), but where more or less impoverishment took place in May or June in the other years, either for a brief period only, or of longer duration (see following Table). Monthly averages, however, for the several years combined of 83 c.c. for February, 31 c.c. for April, 21 c.c. for May, 25 c.c. for June, and 28 c.c. for July (this latter for 1929 only) suggest that volumes less than half as large are the normal expectation through spring and summer than at the end of the winter, but (by the evidence of 1931) with the peak of abundance to be expected in early autumn, when the average may rise above 100 c.c.

Average volumes of *Centropages typicus*

Month	Year	Inshore	Offshore	North	South	Area Surveyed	Maximum	Minimum
February	1930	124	1	12	102	59	915	0
	1931	1	12	1	11	8	76	0
	1932	169	5	8	135	101	459	0
April	1929	24	21	18	27	23	87	<1
	1930	33	13	5	35	21	368	<1
May	1929	14	16	14	16	15	58	0
	1930	33	5	6	26	15	92	0
	1931	1	2	1	1	1	6	0
	1932	17	31	9	42	25	276	0
June	1929	15	12	6	27	14	107	0
	1930	7	1	3	2	3	35	0
	1931	11	7	9	12	10	120	0
	1932	31	22	13	57	32	276	<1
July	1929	59	31	35	28	46	256	0
	1930	208	12	92	—	92	1341	0
	1931	146	11	95	—	95	1070	0
October	1931	—	80	111	32	80	256	<1

In February, of the two years when Centropages occurred in more than minimal numbers in that month, the largest catches were made close to the mouth of Delaware Bay (1932), and from Chesapeake Bay southward (1930). But the locations of the centers of greatest abundance have varied widely, from year to year, during the other months (Fig. 28, 29), and also from year to year. In 1930, for example, the concentration of Centropages that was encountered off Delaware Bay in February had been largely obliterated by April. In May of 1929, the richest concentration (58 c.c.) lay mid-way out on the shelf, on the Martha's Vineyard profile, while in 1932, the more northerly of the two centers where Centropages had been most numerous in February, had broken down by May, whereas the more southerly (off Chesapeake Bay) had persisted, merely shifting some miles northward.

It seems, however, that the rich centers tend on the whole to become more generally distributed from February and April to May, out across the shelf in the sector southward from the offing of New York (to which they are so far confined). And although they may then contract again, in June, if the population be decreasing (cf. Fig. 28 and Fig. 29), centers of abundance may again appear offshore, from June through July, to the north as well as to the south, while the

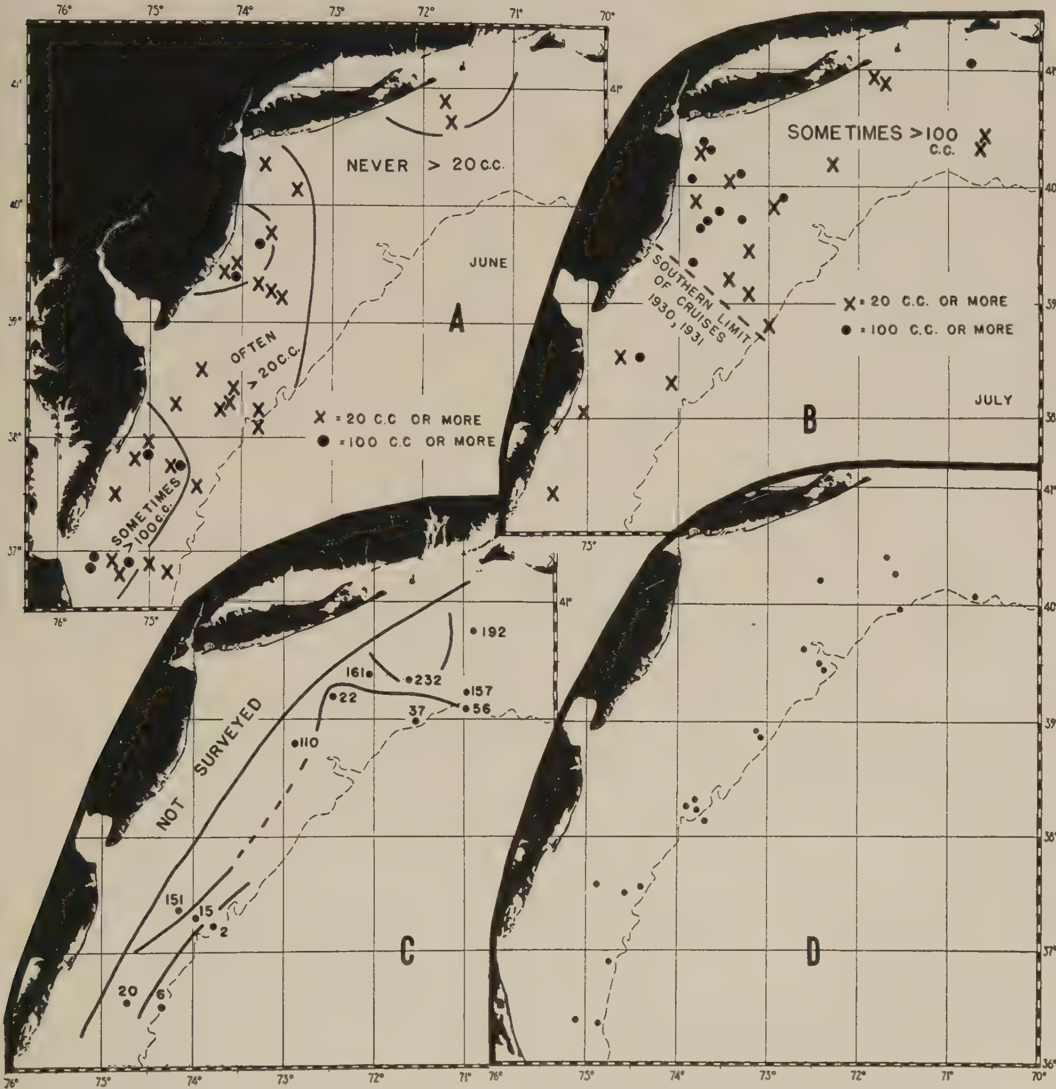

NEVER > 20 C.C.
JUNE
A
OFTEN > 20 C.C.
SOMETIMES > 100 C.C.
X = 20 C.C. OR MORE
● = 100 C.C. OR MORE
SOMETIMES > 100 C.C.
SOUTHERN LIMIT OF CRUISES 1930, 1931
X = 20 C.C. OR MORE
● = 100 C.C. OR MORE
JULY
B
192
161
232
22
157
56
37
110
NOT SURVEYED
151
15
2
20
6
C
D
76°
75°
74°
73°
72°
71°
70°
41°
40°
39°
38°
37°
36°

Fig. 29. Locality records, all cruises combined: A, *Centropages typicus*, large volumes for June; B, *C. typicus*, as above for July; C, volumes of *C. typicus*, per standard haul, October 19–28, 1931; D. locality records for *Centropages violaceus*, all cruises combined.

distribution for October 1931 shows the center of abundance (250 c.c.), as lying off Martha's Vineyard, instead of off New York and off New Jersey as had been the case in the preceding July.

The composite picture is thus of a progressive shift in the situation of the center of population from the Delaware Bay-Chesapeake Bay sector in February-April, progressively northward to the offing of New York in July, and finally by mid-autumn to the eastern boundary of our area. The result is that the volume of *Centropages typicus* may average about as large in the north, at the season of peak abundance there (July-October), as it is in the south in the months when largest there—February-April or June, according to the year. But Centropages has been so much more plentiful south than north in most of the individual months, other than July or October, that the average for the series as a whole is more than twice as large for the southern sector (42 c.c.) as for the northern (17 c.c.). *C. typicus* is therefore to be classed as primarily a southern species in our area. And while it occurs in considerable abundance as far north and east as the Gulf of Maine, it appears that Cape Sable, Nova Scotia, marks its approximate boundary in that direction (Bigelow, 1926, p. 223).

The inshore belt has also averaged from 1.5 to 7 times as productive of it as the offshore in each month, of the several years combined, maximum catches of 400–1000 c.c. or more, not being unusual there, at the season of maximum abundance.

Annual variations. The averages given in the column headed "Area surveyed" in the table on page 322, show that while Centropages may vary widely in abundance from year to year, at the end of the winter (when it has averaged 12–13 times as plentiful volumetrically in the richest year as in the poorest) and also through the spring, it would be a decidedly unusual event for a summer to be either extraordinarily rich or extraordinarily poor in this copepod.

Vertical distribution. In the one February of record, Centropages was distributed with approximate uniformity vertically, at more than half the stations (Fig. 30) and it was as often most plentiful deep as shoal at the others. But the center of abundance was much more often shoal, than deep in each other month, with more than half the stations showing one or the other type of vertical stratification. Similarly, the relative frequency of cases in which the catch was ten times as great from the one level as from the other, fails to suggest any definite vertical gradient in February or April, but enforces the conclusion that in May, June, and July, the zone of chief abundance for Centropages was much more often in the upper 10 meters or so, than at 20 meters or deeper.

On the other hand, the volumetric ratios of deep catch to shoal (listed below) suggest a seasonal reversal, for the deep averaged considerably the more voluminous of the pair on four cruises in February, April, and May, but the shoal the more voluminous on five cruises in May, June, and July.

Average ratio of volume at 10–0 meters to that at 20–40 meters: February, 1932, 1 to 2.5; April, 1929, 1 to 4.8; May, 1929, 1 to 2.3; May, 1931, 1 to 1.1; May, 1932, 1 to 0.6; June, 1929, 1 to 0.6; June, 1931, 1 to 0.7; June, 1932, 1 to 0.6; July, 1929, 1 to 0.5; July, 1931, 1 to 1.0.

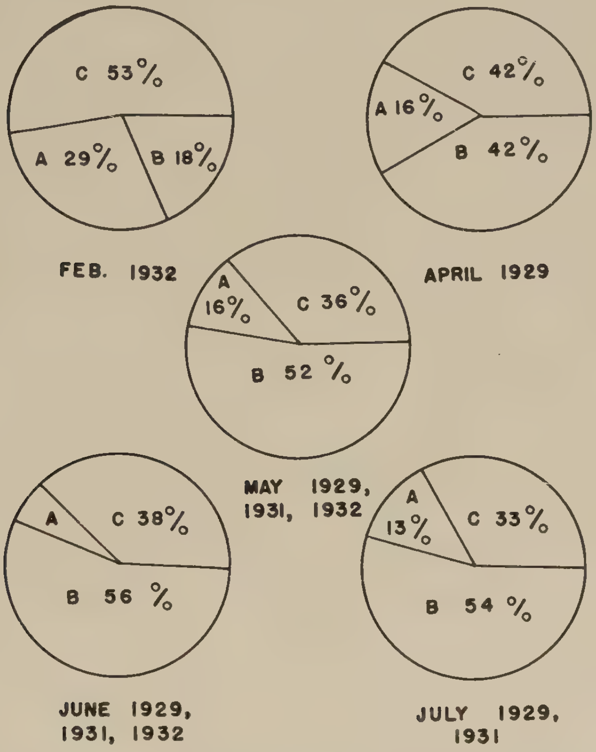


Fig. 30. *Centropages typicus:* percentage of cases, in different months, when the deep catch was twice as large as the shoal (A); in which the shoal catch twice as large as the deep (B); and in which neither catch was twice as large as the other (C).

The danger of confusing regional and temporal gradients with vertical is so great, when the data are so few, that any attempt to harmonize such conflicting pictures, on the basis of present information, seems idle. The most we dare say is that the center of abundance for Centropages through spring and early summer lies much more often in the upper 10 meters than at any considerable depth, while its relative volumetric distribution through the water column is highly variable from time to time and from place to place.

The fact that a considerable proportion of the stock is living in the upper part of the vertical range of temperature from June on, shows that values higher than 18–20° are not unfavorable for Centropages, which added to its considerable abundance in February 1932 in temperatures of 9–13°, is evidence that the vertical gradient of temperature is not an important factor in determining the vertical distribution of this particular copepod.

CENTROPAGES VIOLACEUS

The records for this species have been confined (with three exceptions) to the outermost belt of the shelf, within 15–16 miles of the 200-meter contour (Fig. 29D). And the latitudinal distribution suggests that *C. violaceus* is as apt to stray in across the edge of the continent about as often in the one sector (north or south) as in the other. With so few data (20 localities), we can only say of its seasonal incidence that we have record of it within our limits in February, May, June, and October; based in every case, on scattered specimens.

CORYCAEUS sp.

Wilson (1932a, p. 42) has already reported four species of Corycaeus off Chesapeake Bay. And our records again yielded a scattering of these tiny copepods in the months of February, April, May, June, July, and October, not only in that same general region, but also northward along the edge of the continent to the offing of Delaware Bay (Fig. 31C).

EUCALANUS sp.

Two species of this genus have been identified in the catches, *attenuatus* and *elongatus*, their chief interest, in the present connection being that they are sure indicators of a warm water source (see Wilson, 1932, for summaries of their known distribution). In the case of *attenuatus* the records are concentrated in the southernmost sector (Fig. 31A), where they extend close inshore, both off Chesapeake Bay and off Delaware Bay. To the northward, they are confined to the extreme outer edge of the shelf, though *E. attenuatus* again approaches the land in the Gulf of Maine with the peripheral drift of water from offshore (Bigelow, 1926, Fig. 71). The three records for *E. elongatus* were all well out on the shelf. And juveniles and damaged specimens, of the one species or the other were also detected at the additional stations marked on Figure 31A. All but one of the records for *attenatus* were for the month of April, as were two of the three

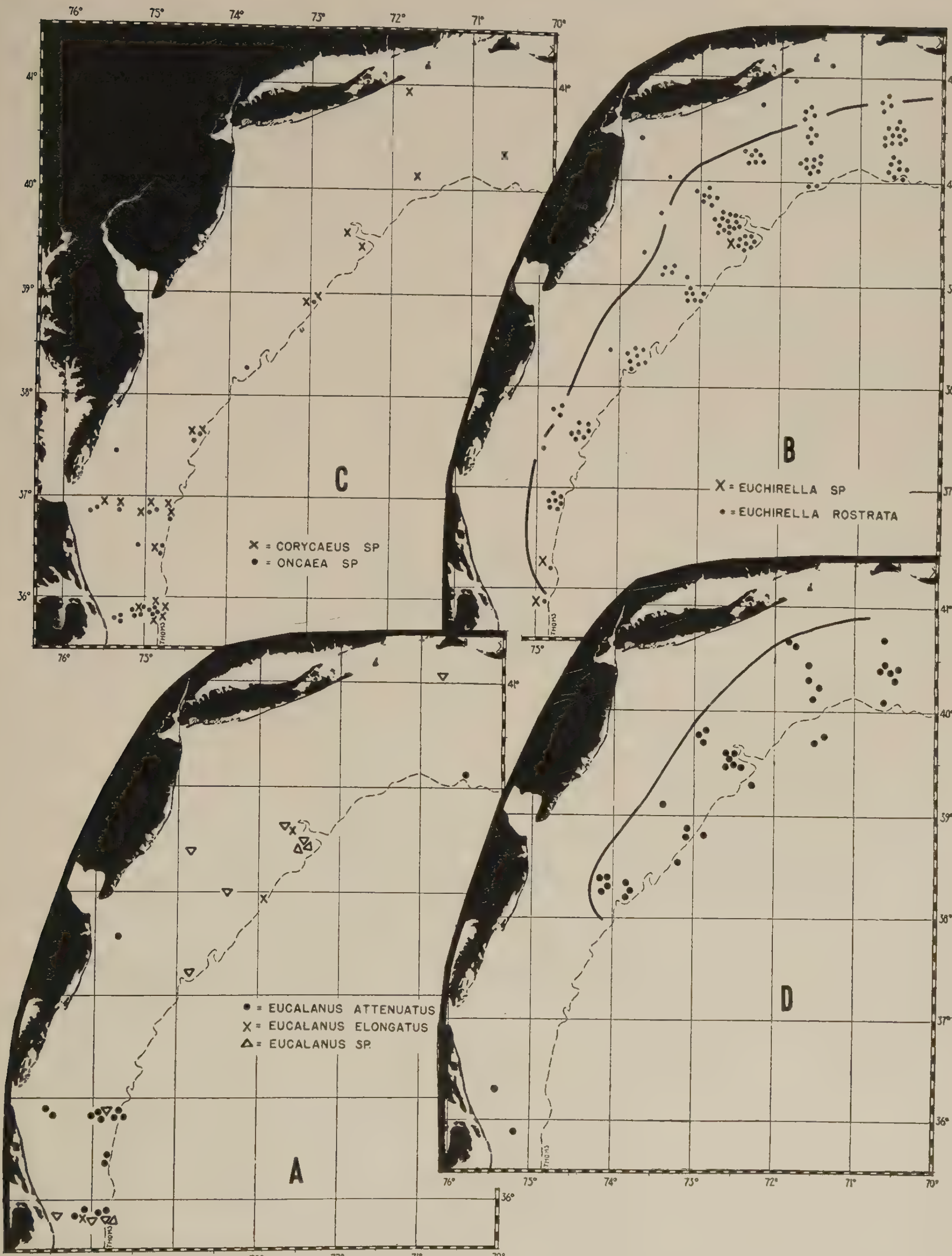

C
× = CORYCAEUS SP
● = ONCAEA SP
B
X = EUCHIRELLA SP
• = EUCHIRELLA ROSTRATA
● = EUCALANUS ATTENUATUS
X = EUCALANUS ELONGATUS
△ = EUCALANUS SP.
A
D
76°
75°
74°
73°
72°
71°
70°
41°
40°
39°
38°
37°
36°
THOMS

Fig. 31. Locality records, all cruises combined: A, *Eucalanus attenuatus*, *E. elongatus* and Eucalanus sp.; B, *Euchirella rostrata* and Euchirella sp. offshore and inshore; C, Corycaeus and Oncaea; D, Volumes of *Metridia lucens* greater than 100 c.c. (solid circles), boundary separating this area from that where the volume was usually less than 5 c.c.

records for *elongatus*, the others for May, whereas Eucalanus of doubtful identity were taken at all seasons.

It is interesting that while *E. attenuatus* occurs but so seldom in our waters and while the largest catch was only 32 c.c., 11 out of the 16 catches were of 1 c.c. or greater, averaging nearly 6 c.c., which suggests that a considerable population of it exists along the continental slope. But the records for *elongatus* were for strays only.

Euchirella rostrata

Previous records of this copepod, west and south of Cape Cod, were confined to the extreme outer edge of the shelf and continental slope (Bigelow, 1915; 1922). The data for 1929–1932 (Fig. 31B) show, however, that while this is distinctly an offshore species within our limits (recorded at 5% only of the inshore stations), it occurs much more generally in the offshore belt there (38% of the stations) than it does in the Gulf of Maine, where it appears to be sharply confined to the chief drift-tracks (Bigelow, 1926, Fig. 71; Fish and Johnson, 1937, Fig. 25). It has also averaged considerably more frequent in the northern sector (26% of the stations) than in the southern (12%) for all cruises combined. And the fact that it was recorded about as frequently, relatively, in one month as another from April to July (17–32% of the stations), but not at all in February, on the one hand, or in October on the other, equally identifies it as a spring and summer species in our waters.

Only two of the catches were larger than 1 c.c., with 6 c.c. as a maximum, all other records being of stray individuals only. Thus, we have no reason to suppose that it ever succeeds in breeding in significant amounts inside the continental edge, even at the warmest season, but rather that its status there is strictly that of a warm oceanic immigrant, which makes it a useful indicator-species.

Mecynocera clausi

It appears that *M. clausi*, like *Centropages violaceus* and *Pleuromamma gracilis*, strays in over the shelf about as frequently in the north as in the south. And the records show that it is as liable to drift farther in than do either of these, as is also the case in the Gulf of Maine, where it has been taken near land, on three occasions (Bigelow, 1926, p. 245). Even for it, however, the great majority of the captures were more than 30 miles from the coast (Fig. 33A). It also occurs, at times, in moderate numbers, for catches of 1–4 c.c. were recorded on 6 occasions, 11 c.c., once. The percentage of stations at which it was recorded

(30% for February, 0% for April, 6–14% for May-July, but 87% for October) may indicate a greater tendency for it to drift shoreward at the end of winter and in autumn than during the intervening period. We suspect, however, that these seasonal differences are evidence of irregular fluctuations, rather than of any definitely seasonal succession.

METRIDIA LUCENS

Frequency. The records for *M. lucens* show wide differences on individual cruises in the frequency and generality of its distribution, the one extreme being illustrated by April, 1929, when it occurred at only 27% of the stations, the other by February 1932, when it was at 88%. Neither does any definitely seasonal cycle appear in this respect for the area as a whole, monthly averages being: 65% for February; 53% for April; 59% for May; 57% for June; 55% for July; and 70% for October.

But Metridia was not only more frequent offshore than inshore in every month and year, as listed below, but was lacking altogether over larger or smaller areas next to the land on most of the cruises. The variations in the inshore boundary to its occurrence have been so considerable from cruise to cruise and from year to year that it is difficult to reduce them to any regular order. In three years, however, out of the four, the barren belt next the land was most extensive in February (1930, 1931) or April (1929, Fig. 32). But Metridia was found close in to the land at one locality or another by May in 1929 and 1931, while in 1930, it was at most of the inshore as well as the offshore stations by the last part of April (Fig. 32). In these same years, this shoreward encroachment was then followed by a retreat from the land, from May to June, most pronounced in 1929 and 1930, but suggested also in 1931. In the fourth year of the series (1932), Metridia was much more general inshore at the end of the winter than in the other years, but was absent from belts of fluctuating extent next the land through May and June.

Frequency ratio of *Metridia lucens* offshore relative to inshore

Month	1929	1930	1931	1932	Average
February	—	1 to 0.3	1 to 0.2	1 to 0.8	1 to 0.4
April	1 to 0	1 to 0.7	—	—	1 to 0.5
May	1 to 0.5	1 to 0.7	1 to 0.2	1 to 0.7	1 to 0.5
June	1 to 0.4	1 to 0.2	1 to 0.6	1 to 0.7	1 to 0.4
July	1 to 0.2	1 to 0.6	1 to 0.6	—	1 to 0.5
Average	1 to 0.3	1 to 0.5	1 to 0.5	1 to 0.7	

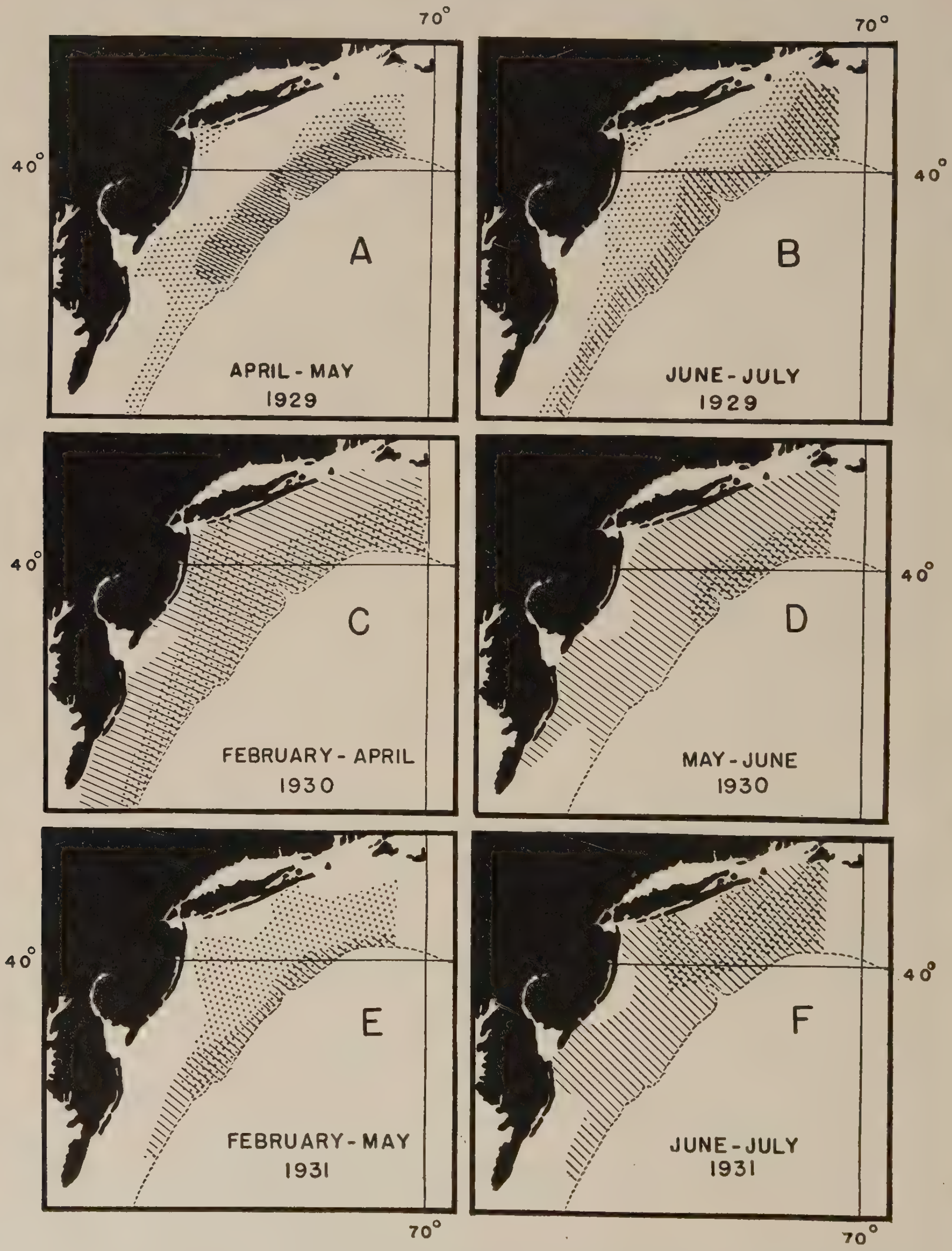

70°
70°
40°
40°
A
APRIL - MAY
1929
B
JUNE - JULY
1929
40°
40°
C
FEBRUARY - APRIL
1930
D
MAY - JUNE
1930
40°
40°
E
FEBRUARY - MAY
1931
F
JUNE - JULY
1931
70°
70°

Fig. 32. Areas of occurrence of *Metridia lucens:* A, April 19–24 (hatched) and May 10–18 (dotted), 1929; B, May 28–June 5 (dotted) and July 11–August 1 (hatched), 1929; C, February 5–13 (dotted) and April 3–May 1 (hatched), 1930; D, May 12–23 (hatched) and June 7–18 (dotted), 1930; E, February 13–March 5 (hatched) and May 16–22 (dotted), 1931; F, June 12–19 (hatched) and July 10–16 (dotted), 1931.

These alternate states suggest that Metridia is to be expected near land only locally, if at all, at the end of a normally cold winter, but that it tends to spread close in to the coast line through considerable sectors at some time in the spring, to disappear again progressively, from parts of the inshore belt, during the summer. After a warm winter, Metridia may, however, be widespread inshore as early as February, and the tendency toward local disappearance from the coastwise belt may become effective as early as the middle of May. Minor or short-period oscillations in the inshore boundary to the occurrence of this copepod, no doubt reflect the appearances and disappearances of successive broods, or incursions from the offshore reservoir where the species is constantly present.

Metridia also averaged consistently more frequent in the north than in the south in spring and summer, in the following ratios:

Frequency ratio of *Metridia lucens*, north relative to south

Month	Year		Month	Year	
February	1930	1 to 1.0	June	1929	1 to 0.4
"	1931	1 to 2.7	"	1930	—
"	1932	1 to 0.8	"	1931	1 to 0.1
Average		1 to 1.5	"	1932	1 to 0.7
April	1929	1 to 0.2	Average		1 to 0.5
"	1930	1 to 0.9	July	1929	1 to 0.8
Average		1 to 0.5	"	1930	—
May	1929	1 to 0.7	"	1931	—
"	1930	1 to 0.7	October	1931	1 to 0.9
"	1931	1 to 0.1			
"	1932	1 to 0.9			
Average		1 to 0.6			

Its frequency indeed, averaged as high at this season (70–100%) as that of Calanus (p. 305) in the northern offshore sector. But the fact that it averaged rather more frequent in the south than in the north in February (3 years) suggests a seasonal reversal in this respect.

Abundance. Metridia averaged considerably more abundant (volumetrically) offshore than inshore, on 15 of the 16 surveys (Table, p. 332), as well as more frequent, the sole exception being in February 1932. And the offshore-inshore ratio of about 5 to 1 that results for the series as a whole is perhaps a reasonable expectation for the vernal six months combined, taking one year with another. The tabulation suggests, however, that there may be some tendency for this regional contrast to reach a maximum in April or May, in which months the ratios of volume offshore to inshore averaged, respectively, about 12 to 1 and about 8 to 1, contrasted with average ratios of about 5 or 6 to 1 in June and July, and about 1.2 to 1 in February.

Average volumes of *Metridia lucens*

Month	Year	Inshore	Offshore	North	South	Area surveyed	Maximum	Minimum
February	1930	<1	6	5	2	6	42	0
	1931	<1	23	2	20	13	78	0
	1932	34	13	7	33	26	165	0
April	1929	0	19	13	3	8	106	0
	1930	16	78	71	26	47	272	0
May	1929	2	6	5	2	4	37	0
	1930	10	68	57	9	36	168	0
	1931	2	59	31	14	26	193	0
	1932	8	47	28	17	25	220	0
June	1929	11	27	11	9	11	210	0
	1930	<1	24	11	2	9	83	0
	1931	6	28	17	9	14	159	0
	1932	5	35	13	13	15	189	0
July	1929	<1	9	6	<1	3	71	0
	1930	<1	23	13	—	13	102	0
	1931	3	6	4	—	4	20	0
October	1931	—	17	26	4	17	104	0

It is not astonishing in view of the foregoing that nearly all the large catches (> 100 c.c.) of Metridia were made more than 35 miles out from land, and north of Latitude 38° (Fig. 31D), the only exception being that two large catches were made close inshore, off Currituck and Bodie Island in February 1932. Equally demonstrative of the offshore nature of Metridia is the contrasting fact that only 18 out of 204 stations, within 20 miles of land yielded volumes as large as 5 c.c., whatever the season of the year, most of these being northward from the offing of Delaware Bay. Indeed, no one of the 32 stations near Chesapeake Bay, or thence northward along the coast of Virginia yielded as much as 20 c.c., while Metridia failed altogether at twenty-five of them, marking this as the most barren region for this species. Unfortunately, no information is available in this respect for autumn, the one October cruise having been confined to the offshore belt. The volume of Metridia has also averaged greater—usually more than twice as great—in the north than in the south in every individual month, April to July, excepting in June 1932, when it averaged about the same in the one sector as in the other. But the fact that an even stronger contrast of the reverse sense obtained in

February, in two years out of the three, suggests a regularly seasonal reversal in this respect. Monthly changes in the volume of Metridia have been so irregular and so small inshore, that the ostensible succession there may not be seasonally significant. But the volume of this copepod has averaged 2–11 times as plentiful (by volume) in the offshore belt in April, May, or June, as in February, in at least three out of the four years, and maximum catches have shown a corresponding monthly contrast, suggesting that more or less vernal augmentation is characteristic for it in the zone of chief abundance.

Maximum volumes of *M. lucens*

Month	1929	1930	1931	1932
February	—	42	78	13
April	106	272	—	—
May	21	168	193	47
June	210	83	159	35
July	71	102	18	—

Present indications are that this offshore augmentation may culminate as early as April (e.g., 1930), or by June, at latest (e.g., 1929), and that it is then usually followed by some impoverishment. In some years (1931, for example), partial recovery then follows in the offshore belt by October. But our failure to find Metridia, at all, in the November catches of 1916 suggests that in other years, it may continue extremely scarce right through the autumn. And we lack quantitative data for December or for January.

Annual variations. The differences that have been recorded from year to year, in the inshore boundary to the regular occurrence of Metridia in different months are discussed above (p. 329). We should also point out that the volume of Metridia averaged rather more than three times as large for the area as a whole in the richest years (average, about 22 c.c. in 1930 and 1931, all cruises combined) as in the poorest (1929, average, about 6 c.c.).

OITHONA sp.

The copepods of this genus are so small (about 0.75–1.5 mm. long when adult) that consequently even its adults may have passed through the nets. And because Oithona never formed as much as 1% of the catch in any subdivision, we have not attempted the time-consuming task of estimating the relative abundance of the two species, *similis* and *brevicornis*, that have long been known to occur in the area.

Oithona, of one species or other, was recorded in the catches at 92% of the stations in February, 59% in April, 51% in May, 36% in June, 53% in July, and 57% in October, proving that it is as regular, and probably as frequent an inhabitant of our area as it is of the Gulf of Maine and Bay of Fundy (Fish, 1936b), also about as frequent, north (49% of the stations) as south (54%), and offshore (48%) as inshore (53%). Oithona must, in fact, be extremely numerous at times, for on one occasion (off Bodie Island, in February 1932), no less than 30 c.c., of these tiny copepods were entangled in our coarse-meshed net. But most of the other catches were less than 1 c.c.—often odd specimens only. And the very strong probability that, in many cases, a good part of the local stock passed through the nets, prevents us from drawing any conclusions as to seasonal variations in abundance, from the monthly variations in frequency of occurrence. As a case in point, we may quote a frequency of 86% on the second June cruise of 1932, contrasting with 0% on the third cruise that same month, evidence, perhaps, of the presence of a strong stock of adults on the one occasion, but of their replacement by juveniles, by the time of the second.

Oithona, being so small, is not likely ever to form any considerable percentage of the volume of the total plankton present in our waters. But from experience elsewhere, and from its frequency of occurrence, it may well be a major item in the local diets of larval fishes.

ONCAEA SP.

The grouping of the localities of capture of the scattering specimens of Oncaea (Fig. 31C) suggests that most of them, at least, belong to the widely distributed pelagic species, *O. venusta*, which Wilson (1932a) has already reported in some abundance over the outer edge of the shelf, off Chesapeake Bay, but not within the latter. Apparently, this is a warm-water stray within our limits. But it may be of greater faunistic importance there, on occasion, than might be suggested by the fact that our records are all based on stray individuals, for our nets did not adequately sample animals so small.

PLEUROMAMMA

Two species of Pleuromamma were detected in the catches, *robusta* and *gracilis*, the only previous reports of which, inside the 200-meter contour, within the limits of the present survey, were near Martha's Vineyard (Wilson, 1932), though both of them enter the Gulf of Maine not infrequently, as strays from the continental slope (Bigelow, 1926; Fish and Johnson, 1937). *P. gracilis* was taken not uncommonly on the outer edge of the shelf (Fig. 33), but only five of the 40 records of it were more than 10 miles in from the 200-meter contour, nor have we any evidence that it ever strays shoreward farther than the mid-belt of the shelf.

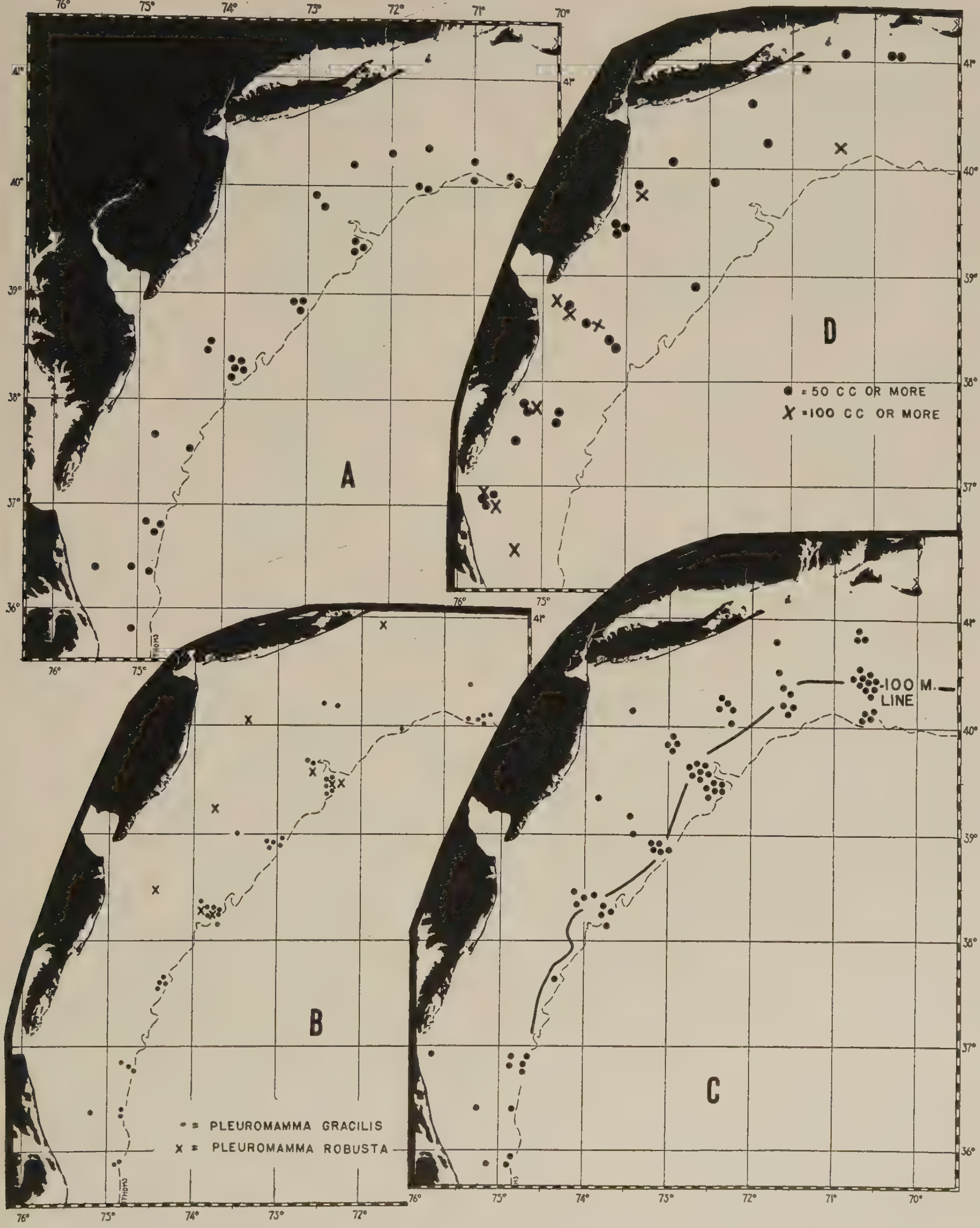

A
B
C
D
● = 50 CC OR MORE
X = 100 CC OR MORE
• = PLEUROMAMMA GRACILIS
x = PLEUROMAMMA ROBUSTA
100 M. LINE
76°
75°
74°
73°
72°
71°
70°
41°
40°
39°
38°
37°
36°

Fig. 33. Locality records, all cruises combined: A, *Mecynocera clausi;* B, *Pleuromamma gracilis* and *P. robusta;* C, *Paraeuchaeta norvegica;* D, large volumes of Pseudocalanus.

P. robusta, on the other hand, was recorded about as often in the inshore belt (4 stations) as offshore (5 stations), once close in to land on the Montauk profile (Fig. 33B).

Since it seems certain that both these species enter our waters from offshore, this distributional contrast suggests that *gracilis* is the more sensitive of the two, to the conditions it encounters in over the shelf.

The monthly distribution of the captures suggests that *P. gracilis* crosses the offshore boundary of the shelf much more often in late winter and early spring, and again in mid-autumn than during the intervening season, for it was taken at 30–37% of the stations in the offshore belt in February, April, and October, but at 17% only in May, and 3% in June and July. Catches of 1 c.c. or more (15 in number) were correspondingly confined to the months of February, April, May, and October. And the fact that the maximum volume of *P. gracilis* was only 10 c.c. (off Montauk, May 21, 1931) is good evidence that it would be a most unusual event for this species ever to develop a rich center within our limits. In the case of *P. robusta,* the captures were confined to the months of February-June. But the number of captures was not large enough to warrant any conclusion as to seasonal gradient within this period. And the records are based in each case on stray specimens.

PARACALANUS PARVUS

This copepod, like Pseudocalanus, is so small that our nets could be expected adequately to sample the adults alone. Even with this reservation, however, the record points to very wide fluctuations from month to month and year to year both in its frequency of occurrence, and in its abundance. In 1929, for example, it was not detected at all in April, May, or June, but was found at 100% of the stations inshore and 62% offshore in July, when it averaged 2 c.c. in volume over the area as a whole. But it seems to have vanished entirely from our area at some time during the subsequent autumn or winter, for it was not found at all in 1930, and at one station only, during the late winter, spring or summer of 1931. But it was at every station visited that October, averaging 62 c.c. in volume. And it may have persisted through the following winter for it was at 86% of the stations in the next February (1932), averaging 26 c.c., and about as frequent in one subdivision of the area as in another. However, it—or its adults, at any rate—had entirely vanished, by the following May and June.

In the absence of any knowledge as to the abundance of its young stages, it is an open question whether these fluctuations in its status are connected with the incidence of successive broods, or whether they are the visible evidence of extreme susceptibility, on the part of this particular species, to the favorability, or the reverse, of its external surroundings. In either case, it is clear that the production of a large crop of adults is a decidedly unusual event within our limits. But when this does occur, which may be either in late winter, in high summer, or in autumn, the resultant volumes may be so large as to make Paracalanus an important item in the total community, for the time being; and perhaps as important in one subdivision as in another, for the concentration of rich catches offshore shown in Fig. 34 may reflect simply the failure to survey the inshore belt in the month (October 1931) when this copepod was the most abundant (p. 336). The largest catches for February were in the south, those for October in the north, the maximum so far recorded being 134 c.c. (Fig. 34).

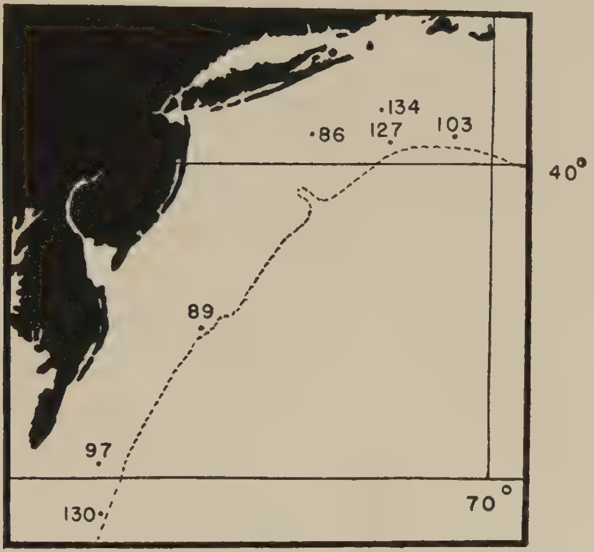


Fig. 34. Volumes, per standard haul, of Paracalanus, all cruises combined.

Paraeuchaeta norvegica

This large copepod—a familiar inhabitant of mid-depths in boreal seas--is one of the most characteristic members of the plankton in the deep basin of the Gulf of Maine, where females with their blue egg clusters are familiar objects, and larvae are plentiful (Campbell, 1934, p. 4, 34). It also occurs with considerable frequency from the offing of Martha's Vineyard westward and southward (Fig. 33C) to that of Chesapeake Bay, outside the 100-meter contour, where Wilson (1932a) also reports it. But it so seldom drifts farther in on the shelf, that while taken at 23% of the stations offshore, it was at only 2% inshore within our limits. When this does happen it is about as apt to be off one part of the coast as off another; stray specimens, indeed, may come close in to the land, and consequently into very shoal water on rare occasions, as may any other oceanic waif.

The percentages of the stations at which *P. norvegica* was taken in the offshore belt in different months point to a rather regular increase in the frequency of its occurrence from February (23%) through April (32%) to May (49%), followed by a decrease in June (14%) and July (12%), leading—by present data—to a complete disappearance from this sector of the shelf in the autumn, for it was not found anywhere inside the 200-meter contour at this season either in 1916 or in 1931. And fluctuations of this sort are of special interest in the case of this particular species, because of its reliability as an indicator of continental slope water within our limits.

Paraeuchaeta has proved entirely negligible from the volumetric standpoint, throughout the entire series of observations, for the records have been of stray specimens only, irrespective of the time of year.

PSEUDOCALANUS MINUTUS

Frequency. Pseudocalanus was detected at about 82% of our stations, evidence that it is one of the most regularly distributed species over the area as a whole, and one of the most nearly universal there. But this copepod is so small (adults average only about 1–1.6 mm. in length) that most of the younger individuals and even a considerable percentage of adults may have passed through the nets. It is therefore possible that an increase in recorded frequency from an average of 79% of the stations in February, to 84% in April, and 92% in May, followed by a decrease to 74% in June and 60% in July, but by a subsequent increase to 73% in October may have been due to seasonal alterations in the relative abundance of the older stages (that were caught) and of the juveniles (that were not), rather than to corresponding fluctuations in the actual frequency of the species.

The average frequency was about the same inshore (80%) as offshore (77%); about the same also for the southern sector as a whole (75%) as for the northern (81%), right down to the offing of Chesapeake Bay, where Pseudocalanus was found at 77% of the stations. But the fact that it proved somewhat less frequent farther south, and was lacking at four out of the five stations near Cape Hatteras

(February 1931), suggests that the southern boundary of regular occurrence for it lies not many miles to the south of the Chesapeake Bay profile, as also for sundry other boreal animals.

Abundance. Pseudocalanus, though so nearly universal, was usually present in only small volumes, as emphasized above (Table, p. 229), in the discussion of the relative importance of different species. In fact, the catch was at the rate of not more than 1 c.c. at about ¼ (109) of the 410 stations where this copepod was recorded, while only eight of the catches were greater than 100 c.c., three greater than 200 c.c., with 560 c.c. as the maximum. But for the reason just stated, it is likely that this understates the actual abundance of this species (see also, Fish, 1936a).

The average catches for the area as a whole parallel the monthly frequencies (p. 338), in showing a slight increase from February (average, 10 c.c.) to April (14 c.c.) and May (15 c.c.) followed by a slight decrease through June (12 c.c.) to July (10 c.c.). And while the record for October is confined to a single year (1931), the low average for that cruise (5 c.c.), as contrasted with the preceding July (14 c.c.), probably represents the normal seasonal cycle, for that year was the most productive of the series for this particular copepod. Adults of Pseudocalanus thus appear to average most numerous over the area late in spring, much less so in autumn, though with some recovery through the winter. And while so few juveniles were taken that they do not figure to any significant degree in this summary, they are individually so small that their omission would not greatly affect the volumetric picture.

Average catches for February-June (1929–1932) combined, of 14 c.c. in the inshore belt, 9 c.c. offshore, 11 c.c. in the northern sector, and 9 c.c. in the southern do not differ, one from the other more widely than might be expected from the roughness of the method. Neither do the small catches made in July of 1929 or 1930 show any definite regional gradient, though the waters in the north averaged some 7 times as productive inshore (21 c.c.) as offshore in that month of 1931. And it is doubtful whether the contrast, between greater abundance in the south (10 c.c.) than in the north (3 c.c.) in the offshore belt in the following October, can be taken as characteristic for the time of year. In short, we have no definite evidence that any one part of the area averages significantly more productive of Pseudocalanus than another. But the distribution of the richer catches and especially of the few that were more productive than 100 c.c. (Fig. 33) suggests that it is rather more common for localized centers of abundance to develop within 30–35 miles of the land than farther out on the shelf.

Average volumes of Pseudocalanus for area surveyed

Month	1929	1930	1931	1932
February	—	10	7	13
April	4	24	—	—
May-June	2	1	31	25
July	1	1	14	—

Annual variations. The volume of Pseudocalanus averaged about twice as large, for the area as a whole in the richest year (1932, 13 c.c.) as in the poorest, at the end of winter, while May and June, combined, show an average some 25–30 times as great in two of the years as in the other two, a range much wider than any seasonal or regional contrast that can be deduced from our data. This marks this species as one of the most variable from year to year, of those that figure regularly in the catches.

It is also interesting that the relative ranking of a given year as to the abundance of this copepod may either continue low or high right through the spring and early summer as happened in 1929 and 1932, or it may be abruptly reversed as happened in 1930, when Pseudocalanus was relatively abundant in February and April, but very scarce from May to July.

RHINCALANUS NASUTUS

Frequency. This offshore copepod has been taken widespread throughout the area at one time or another (Fig. 35A) except in the coastal belt between the New York and Martha's Vineyard profiles, where we have no record of it. But the localities of record have been chiefly concentrated in the offshore belt, as was indeed to be expected, some 61% of the catches on the shelf north of Latitude 36° N., having been made within 30 miles of the 200-meter contour. It is no doubt a corollary to the narrowness of the shelf to the southward, that Rhincalanus appears much more frequently near land, south of Delaware Bay, than to the northward.

Rhincalanus has averaged about equally frequent in February, April, and May, but progressively less so in June and July, and this seasonal decline in the regularity of occurrence takes place both earlier inshore, i.e., between February and April, and is more abrupt there than offshore, with no apparent difference in this respect between the northern and southern sectors, as follows:

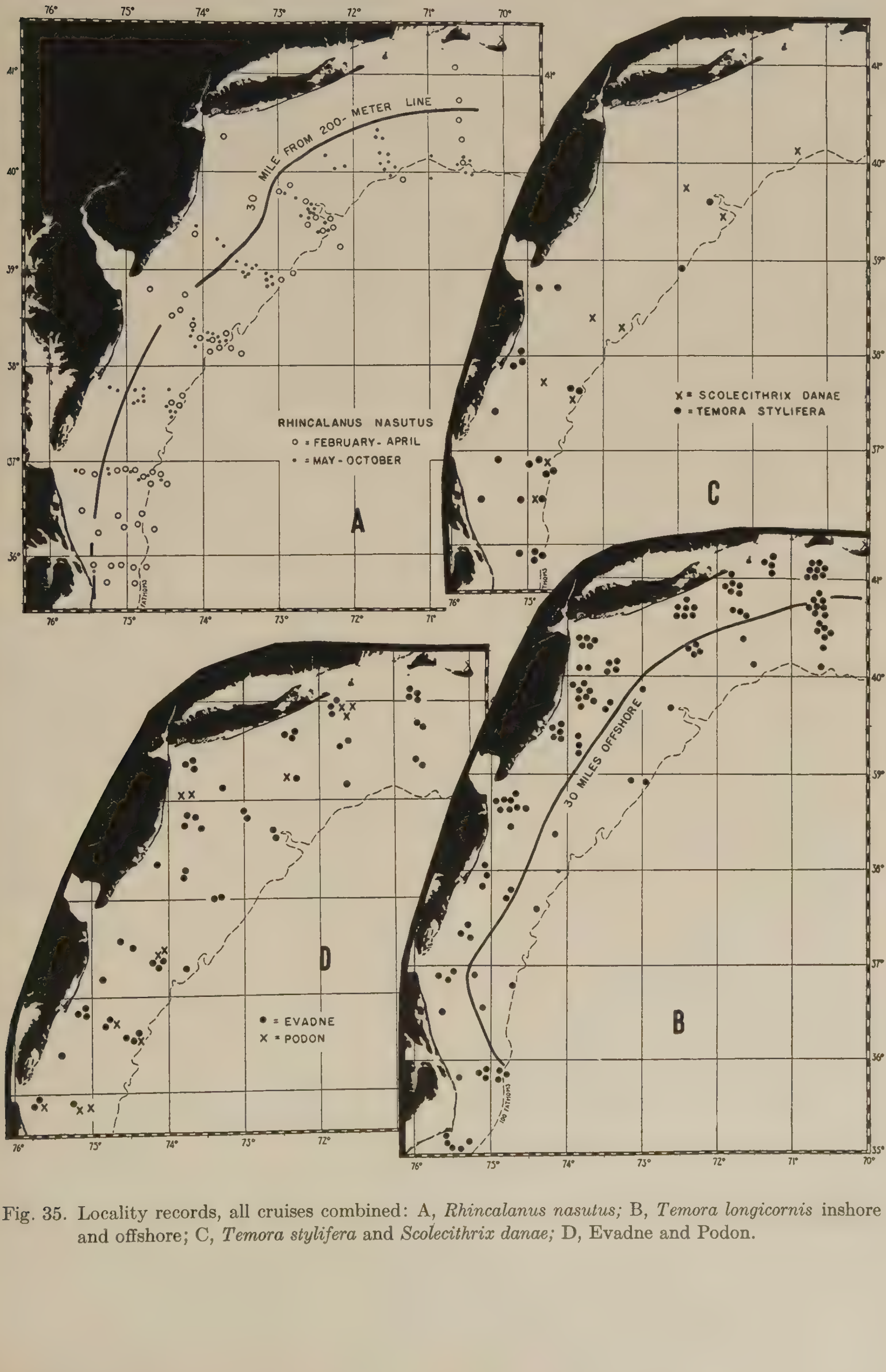

30 MILE FROM 200-METER LINE
RHINCALANUS NASUTUS
○ = FEBRUARY - APRIL
• = MAY - OCTOBER
A
X = SCOLECITHRIX DANAE
● = TEMORA STYLIFERA
C
● = EVADNE
X = PODON
D
30 MILES OFFSHORE
B
100 FATHOMS
76°
75°
74°
73°
72°
71°
70°
41°
40°
39°
38°
37°
36°
35°

Fig. 35. Locality records, all cruises combined: A, *Rhincalanus nasutus;* B, *Temora longicornis* inshore and offshore; C, *Temora stylifera* and *Scolecithrix danae;* D, Evadne and Podon.

Percentage of stations with Rhincalanus

Month	Offshore	Inshore	North	South
February	57%	53%	49%	55%
April	52	4	22	32
May	51	15	25	41
June	37	5	11	31
July	18	0	—	—
October	66	—	—	—

The evidence from 1931 is that the frequency of Rhincalanus rises again during the early autumn in some years—at least in the offshore belt to which the data for that October were confined. But it was not detected at all within our limits in November in 1916, showing that conditions may vary widely in this respect from year to year. We have no information as to the status of Rhincalanus in any part of our area during the first two months of winter.

Abundance. The great majority of the records for Rhincalanus inside the 200-meter contour have been based on occasional individuals, and this large copepod is so easily recognized that the distributional picture is no doubt more nearly complete for it, than for other less conspicuous strays. In fact, Rhincalanus never averaged as much as 1% of the catch for any cruise, even in the offshore belt. A catch of 74 c.c. was made on one occasion, however, with an average of 40 c.c. at three stations near the 200-meter contour from the offing of Delaware Bay to that of Chesapeake Bay (May 2–6, 1932), evidence that it may occasionally be of considerable volumetric importance, within short sectors along the continental edge—doubtless over the slope as well. And when this does happen, Rhincalanus may be expected to form an important item in the diet of any local pelagic fishes, thanks to its large size. Catches of 5 c.c. or more have also been recorded more frequently in the southern sector (8 cases) than in the northern (2 cases).

It appears that Rhincalanus may be expected to invade the shelf in appreciable quantity more often in late spring, than either in winter, on the one hand, or in summer or autumn, on the other, 3 catches larger than 5 c.c. having been made inside the 200-meter line in April, and seven in May, but only one in July and none in October, November, or February.

The distributional picture, as outlined above, seems sufficient ground for concluding that Rhincalanus enters our area only as a stray from the waters of the continental slope. There is no evidence that it can maintain itself, anywhere over the continental shelf north of Cape Hatteras.

Scolecithrix danae

The only previous records of this oceanic copepod off the east coast of North America, with which we are acquainted, are for George's Bank and for the offings of Nantucket and Martha's Vineyard (Wilson, 1932, p. 82). The present records—nine in number and scattered along the offshore belt from the offing of Currituck to that of Montauk—show, however, that it is to be expected anywhere on the outer part of the shelf, within our limits (Fig. 35C). Four out of the nine records are for October, though one cruise (1931) only was made in that month during the four years. The two catches of more than minimal numbers (3 c.c. in each case) that were made inside the 200-meter contour were also in that October, cumulative evidence that this oceanic visitor crosses our boundaries most often in the autumn, but never in any great frequency or abundance.

Temora longicornis

In the winter—by the evidence of 1931—the range of this little brown copepod extends southward to Cape Hatteras (Fig. 35B). And it is possible that this is also true through the spring, for it was found on the Bodie Island profile on each April cruise and off Currituck on the one May cruise (1929) that extended so far south. In June, however, it was taken at but one out of eight stations on the Chesapeake Bay profile, while in July, it was recorded southward only as far as Winterquarter in 1929, as far as Fire Island in 1913, and as far as New York in 1916. While not conclusive, this evidence suggests that the southern boundary to its frequent occurrence tends to recede northward, during the summer, though to different degrees in different years, corresponding to which, it was recorded at 22% of the stations in the northern sector (all cruises combined), but at 14% only in the southern. In the one year (1916), however, when the inshore waters west and south from Cape Cod were visited in autumn, its recorded range extended to the offings of Delaware Bay and of Chesapeake Bay in November (Bigelow, 1922, p. 146).

T. longicornis occurs with some regularity right out to the edge of the continent. But it is much more frequent inshore (26% of the stations) than offshore (11%), which agrees with its status in the Gulf of Maine, where it has its center of distribution inside the 100-meter contour, including in that case the extensive shoal ground of George's Bank (Bigelow, 1926, Fig. 85). It may, in fact, occur as frequently close in to the land as farther out, witness the frequency of records at our innermost stations off Delaware Bay and thence north and east (Fig. 35B), likewise at Woods Hole (Fish, 1925). But available evidence suggests that it does not regularly penetrate estuarine situations along our coasts, unless the renewal of water, from outside, be active, for while it occurs abundantly in Passamaquoddy Bay, tributary to the Bay of Fundy (McMurrich, 1917; Bigelow, 1926; Fish and Johnson, 1937), Cowles (1930) and Wilson (1932a) report it in Chesapeake Bay only at stations near the mouth.

The percentages of the stations at which Temora was recorded north and south, in different months (1929–1932), tabulated below, show it as averaging the most frequent in both sectors in May, followed by impoverishment through the summer, much more extreme in the south—as just outlined—than in the north. The evidence of 1929 and 1930 combined, also is that Temora, in the north, suffers a marked impoverishment for a time in early spring, of which no evidence appears in the south, which can hardly be charged to invasions by eastern water, because Temora is relatively high in frequency in the Gulf of Maine at that same season.

Percentage of stations with *T. longicornis*

	February	April	May	June	July
North	17%	3%	38%	19%	20%
South	13	12	22	12	8[1]

[1] 1929 only.

During the cruises of 1929–1930, only 14 out of the 604 stations yielded catches of Temora as large as 1 c.c., only one as large as 10 c.c., with 13 c.c. as the maximum.

The most interesting feature of these records is that Temora should have invariably been insignificant in the general community, throughout our area, during every cruise, for swarms of it have been encountered close to Martha's Vineyard, July 26, 1916, over Nantucket Shoals, on July 9, 1913, and near Gloucester, on October 31, 1916, while Fish (1925, p. 143) describes the winter samples at Woods Hole as "literally filled with them" in some years. Nor does it seem likely that our nets can have consistently missed the richer aggregations of Temora, characteristic though it be of the latter to form "swarms of great density but of limited extent" (Farran, 1910, p. 72), when one considers that hauls were made at so many stations in different months and years.

We can only conclude that if Temora ever does occur in sufficient volume within our limits to be an important item there, this happens but rarely. And this prevailing scarcity, in the southern part of its range, raises the question of the origin of the local stock, for while we have encountered no centers of active reproduction, the distributional picture is not of a sort to suggest regular immigration, whether out from the coast line, or from the more abundant stocks that exist in winter in the Woods Hole region (Fish, 1925) and in late spring and early summer in the Gulf of Maine.

TEMORA STYLIFERA

The only previous reports of this wide-ranging tropical copepod off the east coast of North America were near Cape Sable, Nova Scotia (Bigelow, 1926, p. 307), and at six "Albatross" stations in the general vicinity of Nantucket and Martha's Vineyard (Wilson, 1932). The records for 1929–1932 now show that it not rarely enters our area, and about equally frequent inshore and offshore (Fig. 35C). But it is so definitely a southern species there that only two out of the 22 captures of it were north of Delaware Bay—both in May—although a considerably greater number of stations were occupied in the northern sector than in the southern. The total number of records for this species was so small (22) that we doubt whether its capture at 50% of the southern stations in July and 19% in April, but at only 2–6% in February, May, or June, and not at all in October, represents any regularly seasonal cycle. The maximum catch, near Winter-quarter, July 1929 was at the rate of 26 c.c., with 6 c.c. and 9 c.c. at two stations off Chesapeake Bay in that same month, evidence that *T. stylifera* may be of faunistic importance locally in the south in midsummer. But the catches in other months were all minimal.

OTHER COPEPODS

The regional distribution of records for other copepods, stray specimens of which were recorded here and there, is summarized in the following table:

Species	Inshore North	Offshore North	Inshore South	Offshore South
Aetidius armatus	0	0	0	3
Calanus minor	0	0	0	1
Undinula vulgaris	0	0	0	1
Calocalanus pavo	1	1	0	1
Centropages furcata	0	0	0	1
Euchaeta marina	0	0	0	1
Eurytemora sp.	1	0	1	0
Eurytemora herdmani	1	0	0	0
Pseudophaenna typica	0	0	0	1
Sapphirina sp.	0	2	0	1

CLADOCERANS

PODON AND EVADNE

The captures of Podon and Evadne do not adequately represent the volumetric status of these little cladocerans of neritic affinity, for they are so small that the greater part of the existent stocks may well have passed through the nets. Nevertheless the records for Evadne, between the offings of Martha's Vineyard, and of Chesapeake Bay, are generally distributed across the whole breadth of the continental shelf, while those for Podon also extend some 40 miles out from the coast (Fig. 35D). This distribution is in striking contrast to the situation as existing in the Gulf of Maine, where they have been seldom found more than 15–16 miles out from land (Bigelow, 1926; Fish and Johnson, 1937), suggesting that coastal water is much more generally dispersed offshore across the shelf west and south of Cape Cod than is the case to the east of the latter.

So far as frequency is concerned, the monthly averages suggest that the winter spores of Evadne do not hatch until well into the spring, but that the peak of abundance for it is reached very soon thereafter, to be followed by a decline in frequency through the summer, for the genus was not recorded at all in February and April, was at 21% of the stations in May, but at only 13% for June, and 7% for July, whereas in the Gulf of Maine the peak is not reached until late summer and early autumn (Bigelow, 1926, p. 307). The data for October 1931, when Evadne was detected at 3 out of 15 stations, would point to a secondary peak in autumn, if accepted at face value. But we hesitate to draw the apparently obvious conclusion, from so small a number of hauls, all from the outer half of the shelf.

The records for Podon are scattered through May, June, July, and October. But they are not sufficiently numerous to warrant deduction as to the seasonal cycle within this period.

The largest catches were at the rates of 6 c.c. and 9 c.c. for Evadne (both in May), of 1 c.c. for Podon, in October, all other records being based on small numbers of individuals.

PENILIA

Penilia schmackeri Richard, was so abundant midway out on the shelf off Cape May on October 23, 1931 (121 c.c.) that it formed 21% of the total catch at one station there, though detected at only one other station off Winterquarter on that cruise, and not at all on any other. Indeed, the only previous record for it on the Atlantic coast of North America is at Beaufort, North Carolina, where according to Sudler (1899, p. 109), it suddenly appeared in swarms during June 1898, to disappear as suddenly. But the fact that it has been reported—always near land—in the Straits of Gibraltar and the Mediterranean, along the east coast of South America, off the west coast of Africa, off the Cape of Good Hope, off India, off Australia, off New Zealand, and off southern China (Gibitz, 1922; Ramner, 1933) shows that it is to be expected anywhere on the continental shelves in warm latitudes, and even in the temperate belt in the warm half of the year.

CHAETOGNATHS

EUKROHNIA HAMATA

Eukrohnia hamata, an indicator of water from mid-depths along the continental slope (Bigelow, 1922, Fig. 50) within our limits, though a regular inhabitant of the deep water of the Gulf of Maine (Bigelow, 1926, p. 328), was recorded at 22 stations scattered along from the offing of Martha's Vineyard to that of Currituck, all but one of them, however, within some 20 miles of the continental edge (Fig. 36A). The seasonal distribution of these records (February, 0; April, 16; May, 4; June, 1; and July, 1) suggests that this species is much more apt to invade our area in early spring than at any other time of year.

In each case, the catch was of stray individuals only.

SAGITTA ELEGANS

Frequency. Sagitta elegans rivals *Calanus finmarchicus* in its frequency of occurrence throughout our area, but it is doubtful whether its range extends farther south than Latitude about 36°, for it was not taken near Cape Hatteras on the winter cruise of 1931, though present at every station to the northward on that occasion. It also corresponds to Calanus in being least frequent on the average in February (67% of the stations, all cruises combined). And while it may be widespread southward past the offing of Chesapeake Bay, at the end of winter, in some years (e.g., 1931), the offing of Delaware Bay may be the southern boundary to its range at that season in others, as was the case in 1932. And the fact that it is the southern margin of its range that most clearly shows these variations from winter to winter, accords with the general rule that it is in the north that it is most abundant, even at times when its distribution is universal to the southward, as well.

In the years when *S. elegans* is scarce or absent in the southern sector at the end of winter, its range expands southward as the season advances, as happened

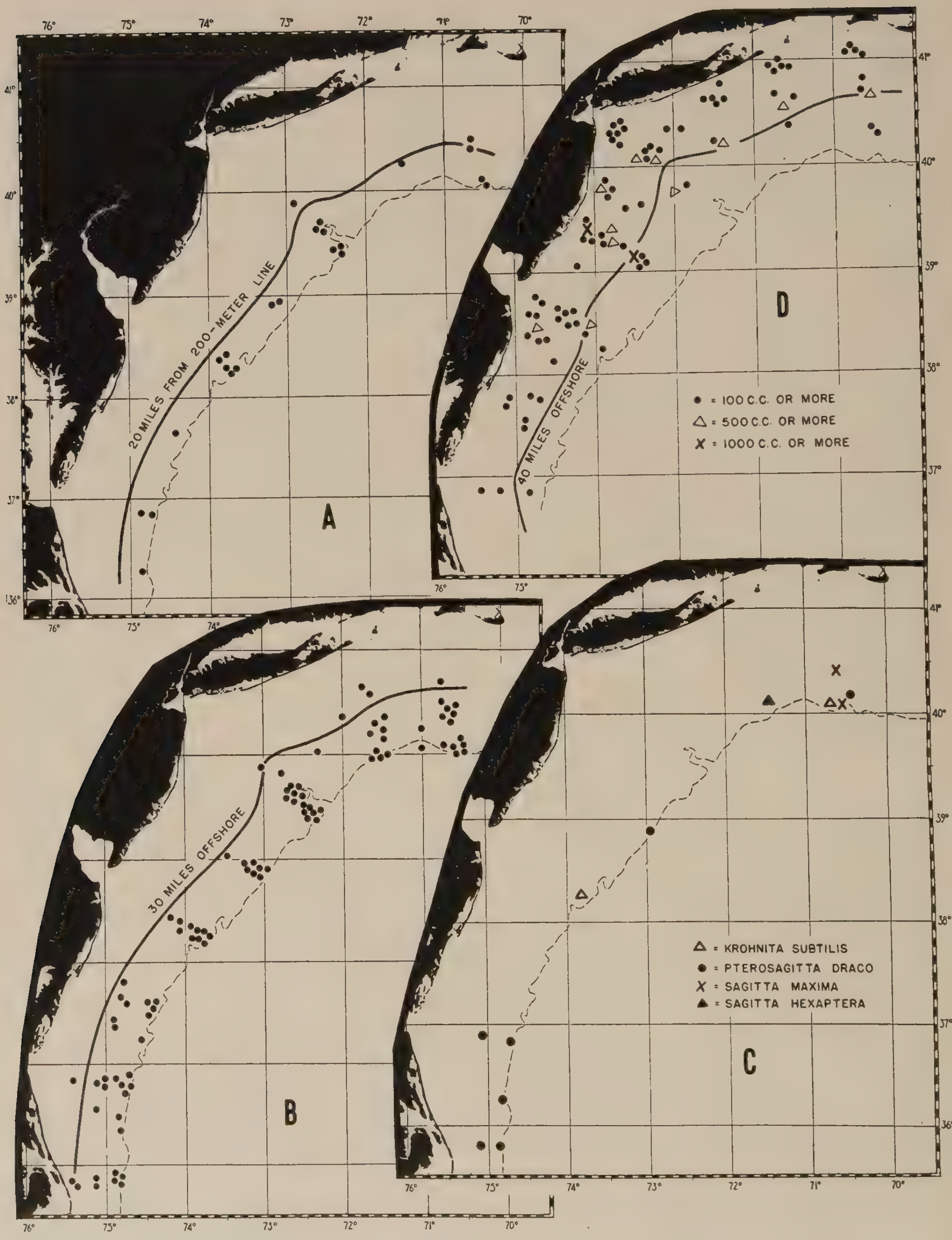

A
20 MILES FROM 200-METER LINE
B
30 MILES OFFSHORE
C
△ = KROHNITA SUBTILIS
● = PTEROSAGITTA DRACO
X = SAGITTA MAXIMA
▲ = SAGITTA HEXAPTERA
D
40 MILES OFFSHORE
● = 100 C.C. OR MORE
△ = 500 C.C. OR MORE
X = 1000 C.C. OR MORE
76°
75°
74°
73°
72°
71°
70°
41°
40°
39°
38°
37°
36°

Fig. 36. Locality records, 1929–1932; A, *Eukrohnia hamata;* B, *Sagitta enflata;* C, *Krohnita subtilis, Pterosagitta draco, Sagitta maxima* and *S. hexaptera;* D, large volumes of *S. elegans.*

in 1929, when its boundary shifted about thirty miles in that direction between the third week of April and the third week of May; and again in 1932, when it was lacking south of Delaware Bay in February, but was taken at scattered stations to the offing of Chesapeake Bay, in May. And its presence at 74% of our stations, for April, and at 89% for May (all cruises combined) is perhaps a fair index to the normal expectation, taking one year with another. *S. elegans* was taken at every station on the continental shelf, in June, down to the offing of Chesapeake Bay in 1929, 1930, and 1931; at 97% of the stations in 1932—as close an approach to universal distribution as is ever likely to obtain for any planktonic animal, over any considerable extent of sea.

In the northern sector, it continues equally frequent into July in some years (1930, 100%; 1931, 95%), nearly as frequent in others (1929, 76%). But the facts that it had disappeared from the inshore stations off Chesapeake Bay between June and July of 1929, that it was lacking both there and near Delaware Bay in the latter month of 1916, that it was not found at all in the southern sector in July of 1913, and that it was lacking at three out of seven stations south from the New York profile in October 1931, show that it tends to become less regular in the southern part of its range from mid-summer to mid-autumn, or even to disappear over considerable areas there at this season. And this accords with Cowles' (1930) report of it as common inside Chesapeake Bay in winter and early spring, but very scarce or even absent there in summer.

In some years, as in 1916, *S. elegans* becomes universally distributed, once more, south to the offing of Chesapeake Bay by November, but its February status (p. 347), indicates that in other years its range may not expand southward again until spring.

The present data fail to show how far *S. elegans* may penetrate the estuaries, or other indentations of the coast. Cowles (1930), however, has already reported that it regularly enters Chesapeake Bay in considerable numbers, through the winter and spring with the drift of saline water near the bottom, and that while its numbers decrease going up the Bay, it may survive, in abundance, in salinities as low, even, as 13‰. Offshore, the boundary to its regular occurrence lies near the 200-meter contour, which accords with its neritic nature in boreal seas generally.

Abundance. In a year when *S. elegans* is relatively abundant in February (e.g., 1931), it may remain at about the same level through the spring and early summer, in the more productive inshore belt, increasing slightly meantime in the less productive offshore belt. But in years when it averages low in abundance in February or April (e.g., 1929, 1930, 1932), a decided augmentation may take place through the late spring, both inshore and offshore, to culminate either in June (1930, 1932), or in July (1929), though with wide irregularity from month to month, and with the richest centers often very small in extent. The fact that the volume of *S. elegans* averaged 30 times as great over the region as a whole, at the peak season, as in the preceding winter in 1932, and 46 times as great in the offshore belt in July as in April, in 1929, gives some measure of the magnitude of vernal augmentation in years of this type, while the rapidity with which the volume of *S. elegans* may increase at a given locality, with the advance of the season, may be illustrated by the following examples:

Station, Martha's Vineyard I, April 3, 1930, 99 c.c.; April 29, 1930, 418 c.c.
New York II, April 10, 1930, 20 c.c.; April 28, 1930, 203 c.c.
Cape May II, April 5, 1930, 1 c.c.; April 24, 1930, 166 c.c.
Martha's Vineyard I, May 19, 1932, 11 c.c.; May 28, 1932, 208 c.c.

At the seasonal peak, the volume of this chaetognath has averaged about 90 c.c. inshore and 40 c.c. offshore, for all years combined.

The evidence of 1931 suggests that an average decrease by about ½ in the average volume of *S. elegans*, is to be expected in the offshore belt, between midsummer and mid-autumn (October). But nothing is known of its quantitative status then, or later in the season, in the inshore belt, except that it was reported in relatively high abundance, in the extreme northeastern sector, in January and February of 1936, by Clarke and Zinn (1937).

The only significant exceptions to the general rule that *S. elegans* has averaged somewhat more abundant volumetrically, in the inshore belt than the offshore, was in 1929, when the reverse was true during May, but with the more usual relationship reestablished in June. Evidently, then, this can be accepted as the normal state, interrupted only for brief periods, in some years, but not at all in others (Table, p. 351). For the series as a whole, the volume have averaged about three times as great inshore (57 c.c.) as offshore (22 c.c.), and large catches (> 100 c.c.) have for the most part, been within 40 miles of land. But the strength of this inshore-offshore contrast has varied so widely from cruise to cruise that calculation of seasonal ratios would not be significant.

The order of north-south contrast has been much less regular, for while *S. elegans* averaged from 10–23 times as abundant in the north as in the south in one year (1929), it was most abundant in the south (though the spread was not so wide) in a second (1931), while a shift in the center of population from the northern sector to the southern took place in the other two years, between February and June in the one case (1930), but between the first and fourth weeks of May in the other (1932).

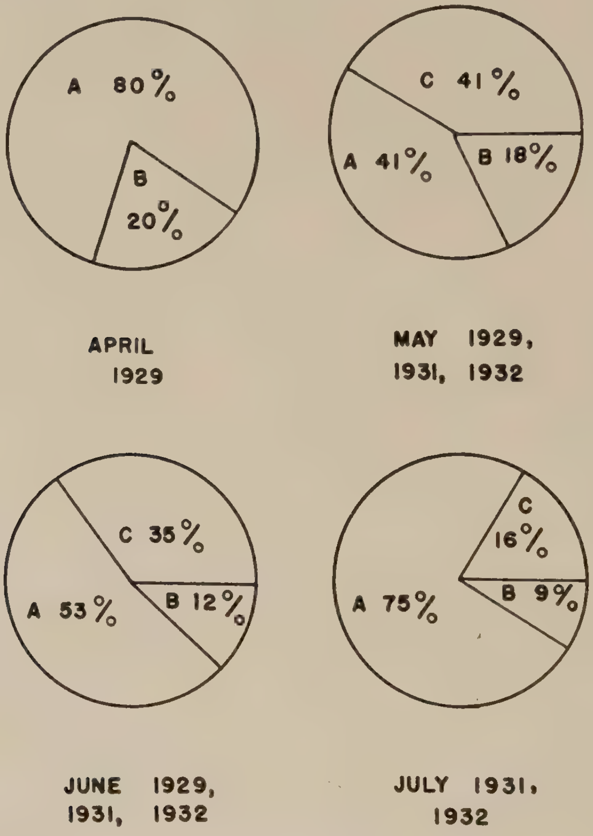
And the catches of 100 c.c. or more (whatever the month or year) have been distributed indifferently, north and south.

Average, maximum, and minimum volumes of *Sagitta elegans*

Month	Year	Inshore	Offshore	North	South	Area surveyed	Maximum	Minimum
February	1930	17	2	19	1	9	87	0
	1931	121	16	29	73	58	431	0
	1932	<1	<1	<1	<1	<1	<1	0
April	1929	10	1	10	0	6	82	0
	1930	37	10	44	8	24	418	0
May	1929	22	35	46	2	25	229	0
	1930	60	37	39	58	49	230	0
	1931	132	19	54	158	84	406	0
	1932	28	12	16	9	18	203	0
June	1929	40	33	55	3	39	217	0
	1930	78	11	34	129	51	1296	0
	1931	136	88	61	225	118	448	<1
	1932	37	15	39	32	31	326	0
July	1929	105	46	81	73	78	520	0
	1930	44	16	27	—	27	129	0
	1931	45	23	37	—	37	242	0
October	1931	—	11	8	16	11	69	0

Annual differences. The fact that 1932 was somewhat the least productive year of the series for *S. elegans* (Table above), 1929 and 1931, on the whole, the most so, suggests that conditions are less favorable for this chaetognath in our area after a warm winter than after a cool. With *S. elegans* averaging nearly 4 times as abundant in some years (1929, 1931) as in another (1932), at the peak season, and more than 58 times as abundant at the end of winter, within a term of four years only, a longer observational series might reveal extremes still further apart.

Sources of the local stock. On the occasions when the boundary of occurrence for *S. elegans* shifts southward from April to June, as happened in the years 1929 and 1932 (p. 349), we may assume that dispersal from the populated waters farther north has been responsible, it being unlikely (in the case of so large an animal) that enough specimens were actually present in the south, early in the season (but passed through our nets) for the local increase to have been the result of their progeny. Cowles (1930), however, has already offered strong evidence that in others years, *elegans* may breed continuously from late winter through the spring as far south as the immediate offing of Chesapeake Bay, though perhaps never within the latter. And it seems sufficiently established that *S. elegans* is regularly endemic farther north, by the facts that the winter and early spring catches have contained a considerable proportion of very small individuals, and that the geographic locations of the richest catches have afforded no evidence of renewals from the waters to the east of our area.



APRIL 1929

MAY 1929, 1931, 1932

JUNE 1929, 1931, 1932

JULY 1931, 1932

Fig. 37. *Sagitta elegans*: percentage of cases in which the deep catch was twice as great as the shoal (A), the shoal catch twice as great as the deep (B), and neither twice as great as the other (C).

Vertical distribution. The deeper catch of *S. elegans* was significantly the larger of the pair much more often than the reverse (Fig. 37) in every month when pertinent data were obtained, except for February (1932), when the numbers were not large enough to be significant in this respect. The extreme case was in April 1929, when *S. elegans* was twice as abundant deep as shoal at 80% of the stations, whereas May 1932 showed the closest approach to vertical uniformity with the deep catch significantly the larger at 35% of the stations, the shoal catch the larger at 21%, and with the one catch about as productive as the other at the remaining 44%.

The volumetric ratio of deep (20–40 meters) catch to shoal (less than 10 meters) has similarly averaged greater than 1 to 1 on every cruise (Table, below), tending to increase from the period April-June (average about 10 to 1) to July, when it averaged 131 to 1 for 1929 and 1931. Catches of 100 c.c. or greater were also made about twice as frequently, relatively, at 10–20 meters (16% of the cases) and at 20–40 meters (16%) as in hauls centering at depths smaller than 10 meters (7%). Thus, it seems sufficiently established that *S. elegans* has its center of abundance in the deeper strata of water below 10 meters. The combined data—if taken at face value—would, in fact, suggest that *S. elegans* averages somewhat the most abundant of all, at depths greater than 40 meters, at least in April, May, and June. But the situation was so variable in this respect from cruise to cruise that the ostensible richness of the deepest strata may perhaps have been caused by the chance that the net encountered rich concentrations of this species at one particular level, but missed them at another.

Average volumetric ratios of *S. elegans* at deeper levels relative to volumes at 10–0 meters

Month	Year	20–40 Meters	No. of Cases	More than 40 Meters	No. of Cases
April	1929	12.3 to 1	6	53.2 to 1	5
May	1929	10.9 to 1	8	48.0 to 1	12
	1931	5.6 to 1	16	1.2 to 1	6
	1932	4.7 to 1	57		
June	1929	10.1 to 1	12	31.3 to 1	11
	1931	32.3 to 1	24	1.2 to 1	3
	1932	6.2 to 1	44		
July	1929	168.6 to 1	10	10.2 to 1	8
	1931	83.0 to 1	14	24.9 to 1	4
Average, April, May, June		11.7 to 1		27.0 to 1	
Average, July		125.8 to 1		17.5 to 1	

The picture as regards diurnal migration is not as clear for *S. elegans*, as it is for *Calanus finmarchicus*, because of wide variability from station to station, in the volumetric ratio of the deeper catch to the shoaler, this having ranged between 540 to 1 and 0.1 to 1, by day, and between 348 to 1 and 0.01 to 1, by night, on one cruise or another. An average ratio, however, of about 37.3 to 1, by day, for April, May, and June[1] (all pertinent stations combined), but of only 5.7 to 1 by night, is evidence of a prevailing tendency for *S. elegans* to sink from the surface by day, to rise again by night, at this season of the year. But the great variability, just emphasized, shows that this tendency is frequently counterbalanced by other factors, probably by movements of the water. Catches made at 3 A.M., 11 A.M., 6 P.M., and 11 P.M., off Fire Island, May 17, 1929, do, in fact, provide as good an example of this for *S. elegans* (Fig. 38) as they do for Calanus (p. 312), for while diurnal migration may explain the impoverishment of the surface recorded between 3 A.M. and 11 A.M., an increase in the ratio of the deep catch to surface catch between 6 P.M. and midnight is not explicable on this basis, nor is the increase that took place between 11 A.M. and 6 P. M. in the total volume of plankton present in the water column as a whole. And the fact that the ratio of deep catch to shoal in July has averaged about the same

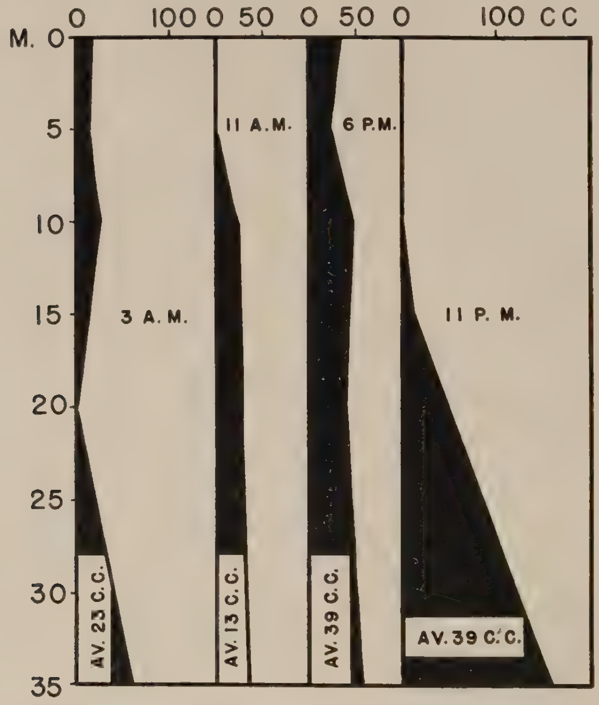


Fig. 38. Vertical distribution of *Sagitta elegans*, near Fire Island, May 17, 1929, at 3:00 a.m., 11:00 a.m., 6:00 p.m., and 11:00 p.m.

---

[1] *S. elegans* was so sparsely represented in February 1932, that this cruise is omitted from the calculation.

by day (65.4 to 1), as by night (61.9 to 1), is sufficient evidence that vertical migrations, of a diurnal sort, are almost entirely prohibited in mid-summer, probably by high temperature.

The vertical thermal gradient in our area is, for the most part so small from February through May that it offers no apparent explanation for the prevailing concentration of *S. elegans* at depths greater than 20 meters, at this season. But the average catches in hauls centering at different temperatures, irrespective of depth, show the following decrease with rising temperature for the several June and July cruises for 1929, 1931, and 1932, combined:

Average volumes of *S. elegans* at different temperatures

Temperature at mid-level of haul	6–8°	8.1–10°	10.1–12°	12.1–14°	14.1–16°	16.1–18°	18.1–20°	>20°
Average in c.c.	52	174	84	59	50	12	4	1
No. cases	37	31	43	39	37	21	30	30

On only four occasions, in fact, was the shoalest catch larger than the next deeper, at a station where the upper 10 meters were warmer than 16°, namely:

Station, New York IV, July 22, 1929, Surface, 21°, 12 c.c.;
58 meters, 8.1° less than 1 c.c.
New York III, June 7, 1932, 8 meters, 16.2°, 21 c.c.;
27 meters, 8.6°, less than 1 c.c.
Cape May III, June 16, 1932, 8 meters, 19°, 38 c.c.;
27 meters, 9.4°, 24 c.c.

This relationship between catch and temperature obviously suggests that the lower values are the more favorable for this species with 18–20° perhaps the upper limit for its continued existence. The warming of the surface thus appears to be the factor chiefly responsible for the rather abrupt rise between June and July, in the volumetric ratio of deep catches of *S. elegans* to shoal (p. 352), just as for Calanus, and likewise for the coincident break-down of effective diurnal migration.

We hesitate, however, to assert that 8–10° is the optimum for *S. elegans*, as the tabulation would suggest if accepted without reservation, for the chance that particular hauls hit or missed rich aggregations may have been partly responsible. And this is made the more likely by the following wide range of volumes from station to station at each temperature interval (irrespective of depth), in the years when hauls were made at two levels or more:

Temp.	6–8°	8.1–10°	10.1–12°	12.1–14°	14.1–16°	16.1–18°	18.1–20°	>20°
C. C.	<1–540	<1–1258	<1–1040	1–823	0–679	0–75	0–38	0–13

SAGITTA ENFLATA

This warm-oceanic chaetognath, already recorded not only along the continental slope, but coastwise south of Delaware Bay (Bigelow, 1915, Fig. 71; 1922, Fig. 50), and even as a stray in Chesapeake Bay (Cowles, 1930, p. 334), was found widespread from the one end of our area to the other, for about 30 miles in from the edge of the continent (Fig. 36B), which brings its area of most frequent occurrence close in to the land to the south of Chesapeake Bay. Northward, however, from Delaware Bay, the coastal belt has usually been bare of it, with the one notable exception that a large catch of juveniles was made close in to Martha's Vineyard in 1935. In this respect, the shelf west of Cape Cod contrasts strongly with the sector next to the east—George's Bank and the Gulf of Maine—where *S. enflata* has not yet been found inside the 200-meter contour.

The distribution of stations does not suggest any greater tendency for this species to enter our area more frequently in the one sector (north or south) than in the other. Its presence, however, at 6% of the stations in the offshore belt in February, at 24% in April, at 31% in May, at 22% in June, and at 15% in July, but at 80% in October, suggests that it invades the shelf least frequently in winter (as was to be expected) and most frequently in autumn, with some tendency toward a second (but minor) peak of frequency in the early spring.

The maximum catch was 66 c.c. off Winterquarter in October 1931, and four other catches of 3–7 c.c. were recorded in that same month. Other than this, the record of it in our waters is based on odd individuals only.

SAGITTA SERRATODENTATA

Frequency. This warm-water chaetognath ranks among the half dozen most generally distributed members of the plankton in the offshore belt, north and south, where it was recorded at 92% of the total stations and at every station on 16 out of the 24 cruises. It was, in fact, at every station throughout the area, as a whole, for February 1930 and 1932. And it has averaged but little less frequent in the inshore belt in the south, than offshore. It has even been recorded occasionally in Chesapeake Bay (Cowles, 1930). But it has been much less frequent close to the land to the northward of Chesapeake Bay, and especially so to the eastward of New York (Fig. 39), where it failed altogether at 54 out of 77 stations.

In the face of this regional contrast, it is interesting and somewhat astonishing that segregation of the data by months fails to suggest any definitely seasonal gradient, in frequency of occurrence, for *S. serratodentata*, whether inshore, where the species is least frequent or offshore, where it is most so. At the most, some decrease may be indicated from February-April to June-July for the inshore belt from New York eastward, but data here are perhaps not numerous enough to warrant definite conclusion.

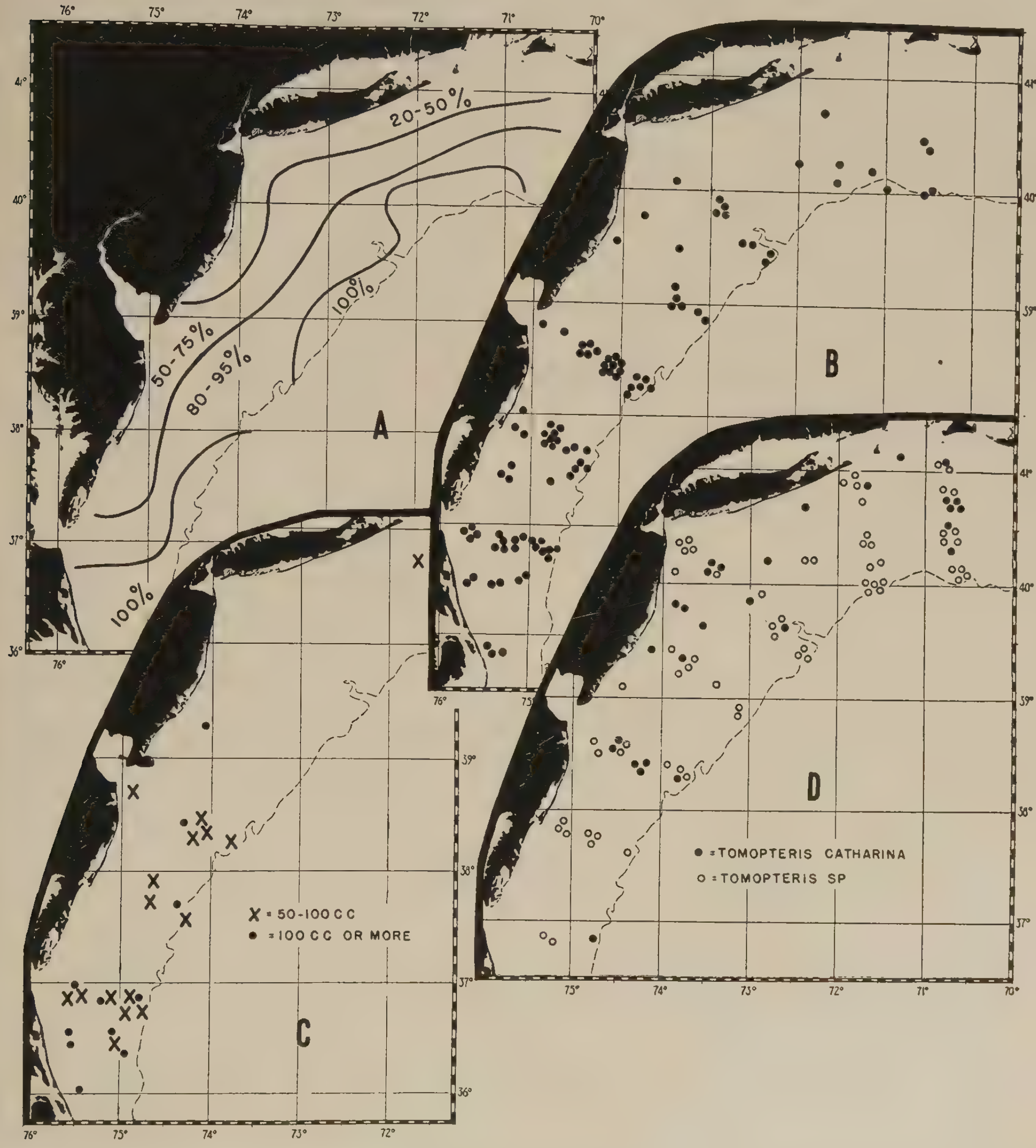

A
B
C
D
20-50%
50-75%
80-95%
100%
100%
X = 50-100 CC
● = 100 CC OR MORE
● = TOMOPTERIS CATHARINA
○ = TOMOPTERIS SP
76°
75°
74°
73°
72°
71°
70°
41°
40°
39°
38°
37°
36°

Fig. 39. A, relative frequency of occurrence of *Sagitta serratodentata* in different areas; B, locality records for volumes of *S. serratodentata* greater than 10 cc.; C, volumes of *S. serratodentata* greater than 50 cc.; D, locality records for *Tomopteris catherina* and for Tomopteris sp.?

Percentage of stations with *S. serratodentata*

Month	Year	Inshore	Offshore	North	South	Area surveyed
February	1930	100%	100%	100%	100%	100%
	1931	57	77	20	91	69
	1932	100	100	100	100	100
April	1929	69	84	46	100	76
	1930	86	100	87	97	93
May	1929	50	64	33	79	52
	1930	86	100	93	91	92
	1931	30	86	58	20	54
	1931	84	92	79	93	84
June	1929	30	64	25	75	43
	1930	36	100	65	50	62
	1931	47	100	62	77	67
	1931	58	93	61	100	72
July	1929	47	81	69	50	63
	1930	59	100	81	—	81
	1931	84	100	90	—	90
October	1931	—	100	100	100	100

Abundance. *S. serratodentata*, while ranking so high in our area in frequency of occurrence, ranks far below its relative, *S. elegans* (Table, p. 351) in volumetric abundance, for the highest average for it in any month was only 53 c.c., even in the subdivision that was richest in it at the time, with a general average, for all regions and months combined of only 12 c.c., contrasted with 225 c.c. and 39 c.c., respectively, for *S. elegans*; 589 c.c. and 144 c.c. for *Calanus finmarchicus*; and 208 c.c. and 37 c.c. for *Centropages typicus*. The maximum catch of *Sagitta serratodentata*—335 c.c.—likewise falls far below that for *S. elegans* (1296 c.c.), for Calanus (1532 c.c.), for Limacina (2666 c.c.), or for Centropages (1341 c.c.).

It is doubtful whether any definite inshore-offshore gradient, in average abundance could be deduced for *Sagitta serratodentata* from our data, for volumes have averaged about as large in the one belt as in the other, both in the south (average, 35 c.c., offshore; 25 c.c., inshore) and in the north (average, 6 c.c., inshore; 5 c.c., offshore), while one very large catch (335 c.c.), close to Atlantic City, on February 8, 1930, was responsible for the only case when any great preponderance was indicated for either sector—inshore, on this occasion. But *S. serratodentata* has on the whole averaged considerably more abundant in the southern sector than in the northern, not only for the series as a whole, but in most of the individual months as well, while in no months was there a strong contrast of the reverse order.

The contrast in this respect between the two sectors may, in fact, average as high as 13 to 1 for a given year as a whole (1931), or 35 to 1 for an individual cruise (February 1931), while the north-south ratio averaged 4 to 1 even in the year (1930) when it was smallest. And the southerly nature of this species is further illustrated by the fact that the rich catches (50 c.c. or more) have been very definitely concentrated from the offing of Delaware Bay southward (Fig. 39B, C). It appears, furthermore, that the northern boundary to common occurrence in abundance is a surprisingly sharp one, for while catches as great as 50 c.c. were made repeatedly on the Cape May profile this seldom happened north of the latter, though an occasional concentration (17–31 c.c.) of *serratodentata* may develop as far east as the Martha's Vineyard profile (e.g., July, 1929), or even in the Gulf of Maine, for that matter.

The volume of *S. serratodentata* in the southern sector, inshore and offshore, has averaged largest either in February or in April, and considerably smaller in May, but with little evidence of any further seasonal alteration through midsummer, while the only high average for the north was also recorded in February. On the other hand, the majority of occasions when *Sagitta serratodentata* has averaged nearly or quite as abundant in the north as in the south have fallen within the period mid-May to October, whereas most of the occasions when there was a notable preponderance of this species in the south have fallen as early as mid-May, or earlier. Averages, for all cruises combined, similarly show the north-south ratio as decreasing from 24 to 1 in February and 18–19 to 1 in April, to 11 to 1 in May, 7 to 1 in June, 1 to 1 in July (one cruise only), and 5 to 1 in October.

The coastal belt from Delaware Bay northward, thus appears more and more nearly to equal the more southerly and offshore waters in suitability as an environment through the late spring and early summer, as the water warms. But it is doubtful whether the small recorded contrast in this respect between July and October is seasonally significant, for the one set of observations was made in one year, the other in another. Neither is information on this point available for the late autumn or early winter.

The regularity of occurrence of this chaetognath, combined with the narrowness of its fluctuations from year to year (p. 360) points to local reproduction rather than to immigration as the chief source of the stock in our waters. And the fact that in 1932 the center of abundance continued in the same region off

Chesapeake Bay from February through the first three weeks in May is further evidence that the coincident decrease that took place in its volumetric abundance during that period was primarily the result of a predominance of death rate over production, not of a mass drift of population away from the locality where it had previously been relatively plentiful.

Average and maximum volumes of *S. serratodentata*

Month	Year	Inshore	Offshore	North	South	Area surveyed	Maximum
February	1930	53	10	36	25	30	335
	1931	55	2	1	35	23	170
	1932	19	15	2	24	18	70
April	1929	26	14	2	37	21	129
	1930	7	10	5	12	8	122
May	1929	4	10	<1	14	7	64
	1930	1	1	9	5	5	230
	1931	<1	1	<1	<1	<1	12
	1932	1	7	1	11	5	98
June	1929	2	4	1	3	3	35
	1930	<1	<1	<1	<1	<1	3
	1931	1	14	<1	15	6	133
	1932	1	7	3	13	6	70
July	1929	2	7	4	5	4	31
	1930	<1	6	3	—	3	31
	1931	7	1	5	—	5	64
October	1931	—	12	5	22	12	69

Annual Variations. The average volumes of *S. serratodentata*, for the area as a whole (including the poorer areas with the richer) and for all cruises for different months combined were 9.5 c.c. for 1929, 9.4 c.c. for 1930, 8.2 c.c. for 1931, and 9.9 c.c. for 1932, a varietal range much smaller than the probable error of observations as rough as ours. And the frequency for any year as a whole was only about 1.4 times as great at the maximum (85%, 1932) as at the minimum (58%, for 1929). Such evidence marks this species as varying much less widely in its status in our area from year to year than do most of the members of the dominant community that are volumetrically more abundant there.

OTHER CHAETOGNATHS

Other species of chaetognaths (*Sagitta hexaptera*, *Sagitta maxima*, *Krohnita subtilis*, *Pterosagitta draco*), recorded over the outer edge of the shelf, at the localities shown on Fig. 36C, D are no doubt to be classed as strays from offshore. In every case, the records are based on occasional individuals.

ANNELIDS

TOMOPTERIS

Tomopteris catharina was taken at localities widely scattered, inshore and offshore alike, from the Martha's Vineyard profile to the Chesapeake profile. And inclusion of the additional locality records for tomopterids probably belonging to *catharina*, but not positively identifiable because of their poor condition (Fig. 39D), would show this species as generally distributed throughout our area between these limits, as it is also in the Gulf of Maine (Bigelow, 1926, Fig. 94), and about as frequent in one subdivision as in another. We have only one record, however, of Tomopteris of any species on the continental shelf, south of Chesapeake Bay, an additional reason for referring the doubtful specimens to *T. catharina.*

Although so general, *T. catharina* appears to be much less frequent, in the waters as a whole to the west of Cape Cod, than it is in the Gulf of Maine to the east, for while it was taken at 38–50% of the stations there, February-May, August, and December-January (Bigelow, 1926), its maximum frequency in our area in any month was only 27%, the average about 14% for all months combined. Monthly frequencies of 20% in February, 4% in April, 21–27% in May-June, and 7% in July and October, also mark it as more definitely seasonal in the southwestern part of its range (with peaks in late winter and in May-June) than it is in the more typically boreal regions to the east and north, where the only indication of any seasonal cycle, yet reported, is an apparent scarcity in late autumn and early winter.

It is interesting that a species so constantly present, and so generally distributed, should never, in all our experience have developed a population abundant enough to yield even one catch as large as 1 c.c., for in the case of so large an animal that would have meant only a few hundred individuals. And the case is similar in the Gulf of Maine, where the catches were "usually from one to half a dozen individuals per haul" (Bigelow, 1926, p. 335).

OTHER ANNELIDS

Annelid worms (not yet identified) were recorded at one station only (off Bodie Island, April 8, 1930). But on that occasion they were in such large volume (47 c.c. or about 24% of the total catch) as to show that they, rarely, may be an item of considerable local importance in the plankton though never (by present evidence) over any considerable area within our limits.

MEDUSAE

AGLANTHA DIGITALE[1]

Regional. At the end of winter the records for Aglantha—scattered, widespread from the offing of Martha's Vineyard, southward to Cape Hatteras—have (with two exceptions) been within 40 miles of the coast. With the advance of the season, it tends to become more frequent inshore, having been recorded at 80–100% of the stations in that belt on each of the May cruises of 1930 and 1932.

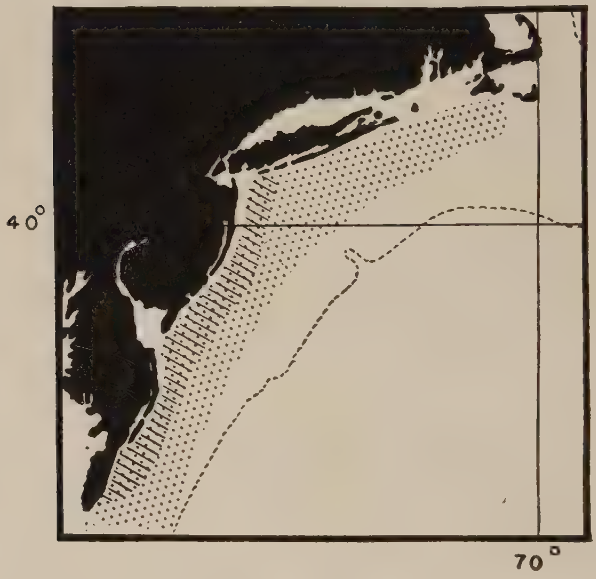


Fig. 40. Areas of occurrence of *Aglantha digitale* in February (dotted) and in April (hatched) 1930.

It appears also characteristic for it to disperse offshore during the last half of the spring, judging from its presence at 57–90% of the offshore stations on those same cruises, and at about the same percentage offshore (46%) as inshore (45%) in that month of 1931. That Aglantha is to be classed as an inshore form in our area (notwithstanding its holoplanktonic nature and wide distribution), also appears in the fact that catches greater than 10 c.c. have (with one exception) been confined to the inshore belt in February, April, and May, though with the offshore boundary for this level of abundance lying some 20 miles farther out to sea for June (Fig. 40, 41). It appears, however, to be about equally frequent north as south, and equally abundant, for the catches, for May, June, and July, combined have averaged about the same in the one sector as in the other (39 c.c., north; 43 c.c., south).

---

[1] For a recent discussion of varietal relationships within this species, see Ranson (1936).

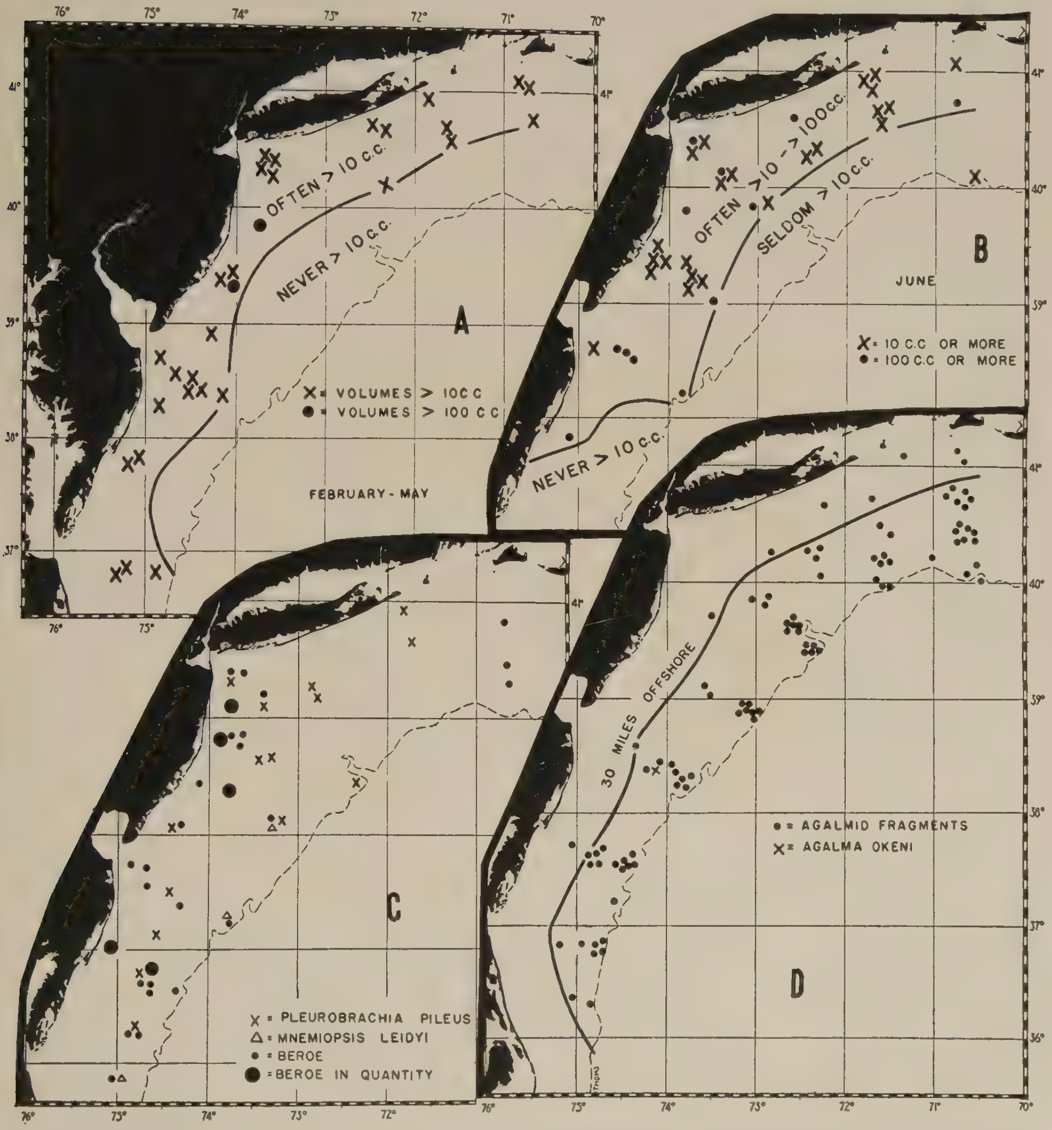

A
OFTEN > 10 C.C.
NEVER > 10 C.C.
X = VOLUMES > 10 C C
● = VOLUMES > 100 C C
FEBRUARY - MAY
B
JUNE
OFTEN > 10 -> 100 C.C.
SELDOM > 10 C.C.
NEVER > 10 C.C.
X = 10 C.C OR MORE
● = 100 C.C OR MORE
C
X = PLEUROBRACHIA PILEUS
Δ = MNEMIOPSIS LEIDYI
• = BEROE
● = BEROE IN QUANTITY
D
30 MILES OFFSHORE
• = AGALMID FRAGMENTS
X = AGALMA OKENI
100 FMS
76°
75°
74°
73°
72°
71°
70°
41°
40°
39°
38°
37°
36°

Fig. 41. A, *Aglantha digitale,* regional abundance, February–May, all cruises combined; B, Aglantha, regional abundance for June; C, locality records for Pleurobrachia and Mnemiopsis and for large and small catches of Beroe, 1929–1932; D, locality records for agalmid fragments and *Agalma okeni.*

Seasonal and annual variations. The fact that Aglantha may appear only sporadically in some years, as in 1929, when it was recognized at two stations only (both in July), but widespread and in considerable volume in others (e.g., 1932), shows that annual variation in its status is wide. More or less vernal augmentation seems, however, to be characteristic for it in its years of abundance. In 1930, for example, it increased in average volume from less than 1 c.c. in April to about 8 c.c. in May-June, while in 1932, the minimal population (average, less than 1 c.c.) existing in early May, was succeeded by average volumes of 56 c.c. inshore, 17 c.c. offshore, 37 c.c. in the north, and 33 c.c. in the south in the succeeding month. Unfortunately, we lack data later in the season, for that particular year. But the facts that Aglantha averaged less than 1 c.c., in any subdivision in July of 1930 and 1931, that it was found only twice west of Cape Cod in the summer of 1913 (Bigelow, 1915), and that the richest catch in October 1931 was less than 1 c.c., added to its apparent absence in 1916, whether in August or in November, marks it as definitely a spring and early summer species, as far as occurrence in significant numbers is concerned.

The very wide annual differences recorded within so short a series of observations, between years (1932), when Aglantha is in high frequency with a very considerable vernal augmentation, as described above, and those (1929), when it is represented within our boundaries by stray individuals only, are most reasonably explained on the assumption that while it may be generally and effectively endemic in some years, it may disappear altogether in others, with repopulation depending on immigration from the east and north.

Average and maximum volumes of *Aglantha digitale*

Month	Year	Inshore	Offshore	North	South	Area surveyed	Maximum
February	1930	2	0	1	1	1	10
	1931	<1	0	<1	<1	<1	<1
	1932	<1	<1	<1	<1	<1	<1
April	1929						
	1930	<1	<1	<1	<1	<1	10
May	1929						
	1930	7	1	3	6	4	32
	1931	<1	<1	<1	<1	<1	<1
	1932	17	8	9	12	11	180
June	1929						
	1930	7	1	5	1	4	62
	1931	<1	<1	<1	<1	<1	2
	1932	56	17	37	33	40	191
July	1929	<1	<1	<1	0	<1	<1
	1930	0	1	<1	—	<1	7
	1931	<1	<1	<1	—	<1	<1
October	1931	—	<1	<1	<1	<1	<1

LEPTOMEDUSAE

A mixed population of small leptomedusae, belonging for the most part to the genus Obelia, call for notice here, since they formed about 1% of the catch in May and June 1932, as well as in July 1929, and 4% in May 1931 (Table, p. 229). In frequency of occurrence these have shown an unmistakable seasonal cycle, for while wholly lacking in February of either year, and at only 3% of the stations in April, they were at 34% in May, and at 18% in June, but at only 10% in July, while they were not taken at all on the one October cruise (1931)—at least in the offshore belt, to which the latter survey was confined.

These medusae have proved much more frequent inshore (24% of the stations, April-July) than offshore (3%), as was to be expected; also more frequent in the north (13%) than in the south (3%).

The average catches, for the months when they occurred in more than minimal numbers, show the same contrast between larger inshore and smaller offshore as do the average frequencies of occurrence; all thirteen of the catches larger than 50 c.c. were, in fact, made inshore. But it is doubtful whether any strong north-south contrast in their abundance, is characteristic, for while catches larger than 50 c.c. were made more often south (10) than north (3), the average volumes were not only somewhat larger south than north as tabulated below, but the largest average volume for either subdivision, in any individual month (May 1931, 32 c.c.) was also in the south.

Average and maximum volumes of Leptomedusae

Month	Inshore	Offshore	North	South	Area surveyed	Maxima
May	11	<1	5	11	6	188
June	3	1	3	2	2	120
July	6	<1	3	5[1]	4	185
Average	7	<1	4	6	4	

In the month of greatest abundance, the average volume of these small leptolines was more than 19 times as great for the area as a whole in the year when they were most abundant (1931, average, 19 c.c.), than in the year (1930) when they were least so; when in fact they were not detected at all though minimal numbers may have actually been present in the water.

---

[1] 1929 only.

Other medusae

Other medusae were negligible from the volumetric standpoint, none other than those mentioned above having formed as much as 1% of any individual catch: nor has time allowed complete identification of the scattered specimens of various species that were included in the catches. We refer the reader to earlier papers (Bigelow, 1915; 1922) for lists of the hydro- and scyphomedusae taken during the summers of 1913 and 1916. Captures of *Laodicea cruciata* off Chesapeake Bay and off Hog Island, in July 1929, added to the locality records for it in the summer of 1913 (Bigelow, 1915, Fig. 79) afford cumulative evidence that this species is widespread in summer well out on the shelf in the southern sector, though apparently it is closely confined to the vicinity of the shore line in the northern, for it was not represented there in any of our July collections, though plentiful at that season along the coasts of southern New England (Mayer, 1910, p. 203). The genus Liriope also proves to occur over the shelf in the southernmost sector in February, as well as in summer, when the inshore species (or race?) *scutigera* is common in and off the southern harbors and bays, while the genus Aequorea—already known to be widespread throughout the area in summer (Bigelow, 1915, p. 319, Fig. 79)—also occurs sparingly in May and June, as well, at least in the southern sector.

SIPHONOPHORES

Agalmidae

Recent towings have shown that one member of this group, *Stephanomia cara*, occasionally swarms in the Gulf of Maine. But we have no evidence that any agalmid is ever of volumetric importance in the planktonic community of the shelf waters west or south of Cape Cod, for while agalmid fragments were recorded at some 93 stations (Fig. 41D), they did not form as much as 1% of the total volume in any subdivision in any individual month. Agalmids appear to be about equally frequent north and south. But the distributional picture shows them to be much more frequent offshore than inshore, in our area, for about 76% of the stations of record, lay in the former belt contrasted with about 24% only in the latter. The seasonal distribution of the records (present at 11% of the stations in February, at 0% in April, at 13–23% in May and June, at 5% in July, and at 93% in October) suggests a decided peak of frequency in autumn, alternating with a period of great impoverishment in the early spring. Previous experience (Bigelow, 1915, Fig. 81) would suggest that in the northern sector, we were dealing with both *Stephanomia cara* and with *Agalma elegans*, and with the latter alone in the southern sector. But the specimens were all in condition so fragmentary (bare stems, or mere remnants of nectophores and bracts), as to prevent identification.

MUGGIAEA KOCHII

The records for this calycophore are confined to the south, one for June, and eight for July, all in the year 1929. In the latter month, the average catch of *M. kochii*, "south," was, indeed, 5 c.c., equivalent to about 2% of the total plankton for that sector at the time (Table, p. 229) with a maximum of 19 c.c. But the fact that it was not recorded at all within our limits, except in the summer of that one year, shows that such invasions occur less frequently off our coasts than they do in the English Channel, where Russell (1934) found it quite regularly, in summer, from 1925 to 1931. We have yet to learn whether *M. kochii* is a reliable indicator—other than of warm water in general—within our limits. It is worth comment, however, that the record (so far as it goes) suggests that *M. kochii* and *M. atlantica* are as mutually exclusive in our area as Russell (1934) has found them to be in English waters, for all our records for the former were in one year (1929), those for the latter in another (1930).

OTHER SIPHONOPHORES

The seasonal incidence of the only other siphonophores that were taken at more than two stations each, was as follows:

Abylopsis tetragona, February, 5 stations; May, 2 stations; July, 1 station; October, 1 station.
Bassia bassensis, February, 1 station; May, 2 stations; June, 3 stations.
Lensia conoidea, May, 6 stations; June, 4 stations; July, 3 stations; October, 2 stations.
Muggiaea atlantica, February, 3 stations; April, 5 stations; all in 1930.

Most of the localities of capture for each of these lie close to the 200-meter contour, and this applies equally to the few other members of the group that were recorded within our limits (Fig. 42). In most cases, the records of siphonophores other than agalmids and *Muggiaea kochii* have been based on odd specimens only.

The Portugese man-of-war (Physalia) drifts in to the coast, near Woods Hole, in considerable numbers in some years, in summer or early autumn after strong southerly winds. And we have heard reports of them at various localities in on the shelf to the southward. Velella and Porpita have also been recorded at Woods Hole and Newport, Rhode Island (Sumner, Osburn, and Cole, 1904, p. 574). None of these genera have any real place, however, in the plankton of our area, except as waifs from tropical waters; neither were any of them represented in the present collections.

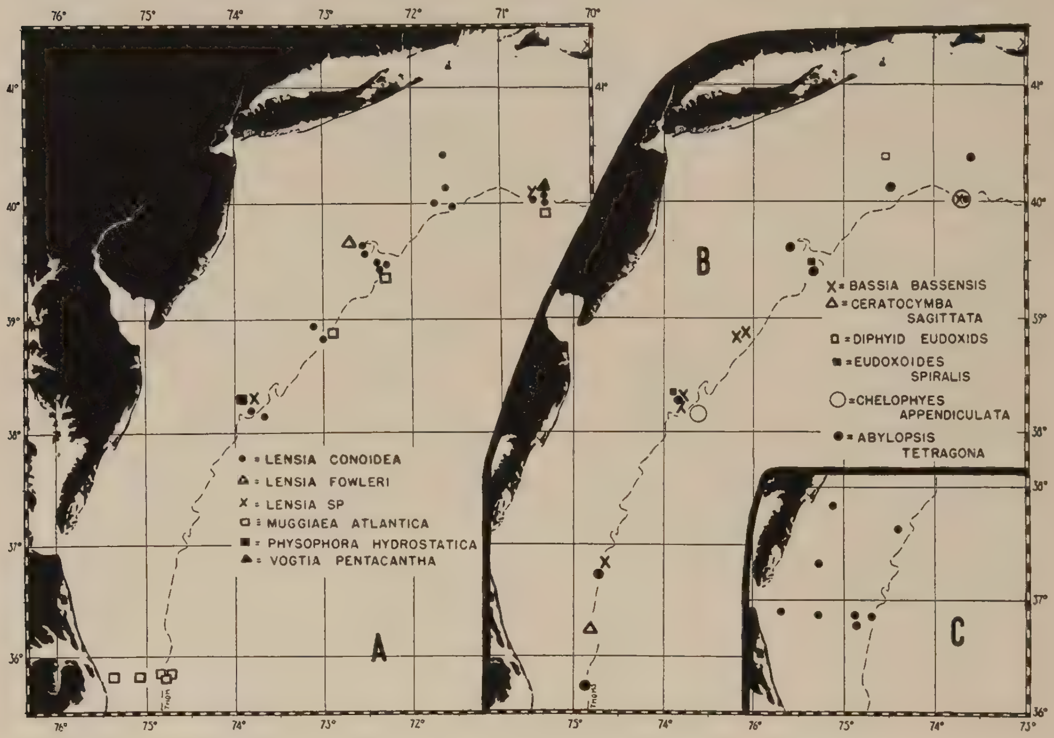

76°
75°
74°
73°
72°
71°
70°
41°
40°
39°
38°
37°
36°
● = LENSIA CONOIDEA
▲ = LENSIA FOWLERI
X = LENSIA SP
□ = MUGGIAEA ATLANTICA
■ = PHYSOPHORA HYDROSTATICA
▲ = VOGTIA PENTACANTHA
A
B
X = BASSIA BASSENSIS
△ = CERATOCYMBA SAGITTATA
□ = DIPHYID EUDOXIDS
■ = EUDOXOIDES SPIRALIS
○ = CHELOPHYES APPENDICULATA
● = ABYLOPSIS TETRAGONA
C

Fig. 42. Locality records, all cruises combined: A, *Lensia conoidia*, *L. fowleri*, *Muggiaea atlantica*, *Physophora hydrostatica*, and *Vogtia pentacantha;* B, *Bassia bassensis*, *Ceratocymba sagittata*, dyphiid eudoxids, *Eudoxoides spiralis*, *Chelophyes appendiculata*, *Abylopsis tetragona;* C, *Muggiaea kochii.*

CTENOPHORES

Beroe sp.

Our records for Beroe are based chiefly on field notes in the station log books, and on fragments battered beyond specific recognition. Previous experience justifies us, however, in assuming that the two species, *cucumis* and *forskalii*, were both represented in the catches (Bigelow, 1915, p. 316; 1926, p. 372).

The earlier record of Beroe within our limits was confined chiefly to the offing of Chesapeake Bay, where *B. forskalii* was abundant in July in 1913 and

1916. Since that time, Beroe has been reported at a number of stations thence northward to New York and again in the offing of Martha's Vineyard, though once only in the intervening sector. The records include February, May, June, and July—there are none for April or for October—but large catches were noted in the log only in June (3 instances) and in July (1 instance). And they were likewise concentrated regionally, inshore, between the Atlantic City and Winter-quarter profiles (Fig. 41C).

The most we dare to hazard from the foregoing is that Beroe may occasionally multiply to great abundance in the inshore belt, between the offings of Chesapeake Bay and of Atlantic City, most frequently toward the south, perhaps due to the influence of the outflow from Chesapeake Bay, nor have we any evidence that Beroe is ever an important factor in the plankton of the northeastern sector of our area, or of the offshore belt, south or north. Rich aggregations of Beroe seem, also, to be confined to the summer months, suggesting that *forskalii* is the species chiefly responsible.

PLEUROBRACHIA PILEUS

During the summer of 1913, this familiar ctenophore was taken at all but two of the stations over the shelf, and in such abundance in the inshore belt between the New York and Cape May profiles that it practically monopolized the deeper water layers there. In 1916, however, the "Grampus" had it at but four stations within our limits at this same season, once only in any abundance (off Chesapeake Bay), and not at all in that November, while it was detected at only 16 of the 604 stations for the period 1929–1932 (Fig. 41C). Definite record of it within our limits has also been confined so far to May, June, and July-August, whatever the year.

As already remarked Pleurobrachia may have been "more widespread in small numbers than these captures suggest, such a fragile organism being easily destroyed in the mass of unsorted plankton" (Bigelow, 1922, p. 158). Nevertheless, the evidence seems sufficiently convincing that while this ctenophore is to be expected anywhere within our limits—offshore and inshore alike—and while it sometimes multiplies enormously, locally, near land, such events are unusual, and perhaps confined to summers of such years as 1913, when the surface waters warm to a temperature somewhat higher than usual. For a further discussion of the local status of this ctenophore, see Bigelow, 1915, p. 321.

Other Ctenophores

In the summer of 1913, the large lobate ctenophore, *Mnemiopsis leidyi*, was not only distributed generally over the inshore belt southward from Barnegat, but swarmed in the surface waters near the coast between that point and Cape May to the practical exclusion of everything else, as described elsewhere (Bigelow, 1915, p. 323). It was again encountered in abundance locally, in that same general region in August 1916, though its observed range was then restricted to the vicinity and offing of Delaware Bay (Bigelow, 1922, p. 158). And the fact that it has been reported near Woods Hole in every month in the year (Sumner, Cole, and Osborne, 1904, p. 579) points to its constant presence in greater or lesser number and at one stage of development or another, along the inshore belt in general.

Unfortunately, the catches for 1929–1932, add nothing to the foregoing, for if they did originally contain any representation of Mnemiopsis, the latter had been battered beyond recognition before the collections were examined, either in the nets, or among the other more resistant animals after capture. And while "Mnemiopsis" is occasionally named in the station log book, the specimens in question may actually have been some other lobate genus.

The positive record for Mnemiopsis is, however, sufficient to show that it is likely to play a very important role in the general planktonic community over considerable areas in the inshore belt at least near the surface, in any year when summer temperatures are relatively high, and locally even in years when temperatures are relatively low. But we have no definite record, as yet, of such a happening to the eastward of New York, except close in to the coast, as at Woods Hole, where Mnemiopsis swarms in some summers. Neither have we any reason to suppose that the adult Mnemiopsis ever occurs beyond the Martha's Vineyard profile, unless as a stray destined to perish in the colder waters of George's Bank, of Nantucket Shoals, or of the Gulf of Maine, to which a drift in that direction would carry it, but where it has never been recorded. If, however, low temperature be actually the barrier to its dispersal in that direction, we must assume that the young stages of this ctenophore are much more resistent to low temperature than is the adult, else this species could not survive the winter chilling to which the waters of the continental shelf are yearly subjected, southward to Chesapeake Bay. Mnemiopsis appears also to be definitely neritic in habit, for while it has been recorded well out on the shelf (Bigelow, 1915, Fig. 80), the largest catches of it were made near shore. During the summer of 1913, when Mnemiopsis was more abundant than at any other time during our observational series, it was taken only close to the surface, which accords with its frequent abundance, right in to the tide line around Woods Hole. Consequently, "the swarms of Mnemiopsis and of Pleurobrachia were mutually exclusive" (Bigelow, 1915, p. 324).

The evidence at hand that adult Mnemiopsis is not abundant—if it occurs at all—in waters colder than about 20°, or more than a few miles out from the coast inclines us to believe that lobate ctenophores of large size, six liters of which were reported in the log book (under the name "Mnemiopsis"), as taken near the outer edge of the shelf off Cape May on May 15, 1929, and as clogging the nets midway out, off Chesapeake Bay, two days later, actually referred to the northern species, *Bolinopsis infundibulum*, which has long been known to abound from Arctic Seas southward to the Gulf of Maine (Bigelow, 1926, p. 372) on our side of the Atlantic.

PROTOZOANS

Our nets were too coarse of mesh for sampling any but the largest protozoa. But the catches made off Bodie Island and off Currituck in May 1929 yielded a few Noctiluca, which had already been found in great abundance at the mouth of Chesapeake Bay in November 1916 (Bigelow, 1922, p. 163); cumulative evidence that it is of widespread occurrence in the southernmost sector, in late spring and autumn. This agrees with its status in Chesapeake Bay, where it is most plentiful at this season, and least so in January and March (Cowles, 1930, p. 328).

BIBLIOGRAPHY

APSTEIN, C.

1906. Plankton in Nord- und Ostsee auf den deutschen Terminfahrten. Wiss. Meeresuntersuch. Komm. wiss. Untersuch. deutsch. Meere, Abt. Kiel, N. F., Vol. IX, pp. 1–25, 14 figs., 10 tables.

BEEBE, WILLIAM

1929. Deep Sea Fish of the Hudson Gorge. Zoologica. Sci. Contr. N. Y. Zool. Soc., Vol. XII, No. 1, 19 pp., 1 textfig.

BIGELOW, H. B.

1914. Oceanography and Plankton of Massachusetts Bay and Adjacent Waters, November, 1912-May, 1913. Bull. Mus. Comp. Zool., Vol. LVIII, No. 10, pp. 385–419, 7 textfigs., 1 pl.

1915. Exploration of the Coast Water between Nova Scotia and Chesapeake Bay, July and August, 1913, by the U. S. Fisheries Schooner Grampus. Oceanography and Plankton. Bull. Mus. Comp. Zool., Vol. LIX, No. 4, pp. 151–359, 82 textfigs., 2 pls.

1922. Exploration of the Coastal Water off the Northeastern United States in 1916 by the U. S. Fisheries Schooner *Grampus*. Bull. Mus. Comp. Zool., Vol. LXV, No. 5, pp. 87–188, 53 textfigs.

1926. Plankton of the Offshore Waters of the Gulf of Maine. Bull. U. S. Bureau of Fisheries, Vol. XL, 1924 (1926), Part 2, pp. 1–509, 134 figs.

1933. Studies of the Waters on the Continental Shelf, Cape Cod to Chesapeake Bay. I. The Cycle of Temperature. Papers in Physical Oceanogr. and Meteorol., Vol. II, No. 4, 135 pp., 66 textfigs.

BIGELOW, HENRY B., and SCHROEDER, WILLIAM C.

1939. Notes on the Fauna above Mud Bottom in Deep Water in the Gulf of Maine. Biol. Bull., Vol. LXXI, No. 3, p. 303-324, 8 textfigs.

BIGELOW, HENRY B., and SEARS, MARY

1935. Studies of the Waters on the Continental Shelf, Cape Cod to Chesapeake Bay. II. Salinity. Papers in Physical Oceanogr. and Meteorol., Vol. IV, No. 1, 94 pp., 55 textfigs.

1937. Siphonophorae. Rep. Dan. Ocean. Exp. 1908–1910 to the Mediterranean and Adjacent Seas, Vol. II, Biology, H. 2, 144 pp., 83 textfigs.

BIGELOW, HENRY B., and WELSH, WILLIAM W.

1925. Fishes of the Gulf of Maine. Bull. U. S. Bureau of Fisheries, Vol. XL, 1924 (1925), Part I, 567 pp., 278 figs.

BOSCHMA, H.

1936. Biological data. Snellius-Exped. in the Eastern Part of the Netherlands East-Indies 1929–1930, Vol. VI, 29 pp., 11 textfigs., 1 chart.

BÜSE, THEODOR

1915. Quantitative Untersuchungen von Planktonfängen des Feuerschiffes "Fehmarnbelt" vom April 1910 bis Marz, 1911. Wiss. Meeresuntersuch. Komm. wiss. Untersuch. deutsch. Meere, Abt. Kiel, N. F., Vol. XVII, pp. 229–280, 3 textfigs., 7 tables.

BRANDT, K.
1898. Beiträge zur Kenntniss der chemischen Zusammensetzung der Planktons. Wiss. Meeresuntersuch. Komm. wiss. Untersuch. deutsch. Meere, Abt. Kiel, N. F., Vol. 3, pp. 43–90, Tables A-G.

CAMPBELL, M. H.
1934. The Life History and Post Embryonic Development of the Copepods, *Calanus tonsus* Brady and *Euchaeta japonica* Marukawa. Jour. Biol. Board Canada, Vol. 1, No. 1, pp. 1–65, 18 textfigs.

CLARKE, GEORGE L., and ZINN, DONALD
1937. Seasonal Production of Zoöplankton off Woods Hole with Special Reference to Calanus finmarchicus. Biol. Bull., Vol. LXXIII, No. 3, pp. 464–487, 7 textfigs.

CONSEIL PERMANENT INTERNATIONAL POUR L'EXPLORATION DE LA MER
1904. Bulletin des Résultats acquis pendant les courses périodiques. Année 1903–1904, 230 pp.
1905. Bulletin des Résultats acquis pendant les courses périodiques. Année 1904–1905, 195 pp.
1907. Bulletin Trimestriel des Résultats acquis pendant les Croisières périodiques et dans les Périodes intermédiares. Année 1906–1907, No. 1, Juillet-Septembre 1906, Part D, 38 pp.

COWLES, R. P.
1930. A Biological Study of the Offshore Waters of Chesapeake Bay. Bull. U. S Bureau of Fisheries, Vol. XLVI, 1930, pp. 277–381, 16 textfigs.

DAMAS, D.
1905. Notes biologiques sur les Copépodes de la Mer Norvégienne. Publ. Circ., No. 22, Cons. Perm. Int. Expl. de la Mer, 23 pp., Pl. 1.

DELFF, CHRISTIAN
1912. Beiträge zur Kenntniss der chemischen Zusammensetzung wirbelloser Meerestiere. Wiss. Meeresuntersuch. Komm. wiss. Untersuch. deutsch. Meere, Abt. Kiel., Vol. XIV, pp. 51–81.

FARRAN, G. P.
1910. Copepoda (Part). Resumé sur le Plankton des Mers. Bull trimestr., Cons. Perm. Int. Expl. de la Mer, Part 1, 1910 pp. 60–80, Pls. VIII-X.

FISH, CHARLES J.
1925. Seasonal Distribution of the Plankton of the Woods Hole Region. Bull. U. S. Bureau of Fisheries, Vol. XLI, 1925, pp. 91–179, 81 textfigs.
1936. The Biology of Calanus finmarchicus in the Gulf of Maine and Bay of Fundy. Biol. Bull., Vol. LXX, No. 1, pp. 118–141, 11 textfigs.
1936a. The Biology of Pseudocalanus minutus in the Gulf of Maine and Bay of Fundy. Biol. Bull., Vol. LXX, No. 2, pp. 193–216, 9 textfigs.
1936b. The Biology of Oithona similis in the Gulf of Maine and Bay of Fundy. Biol. Bull., Vol. LXXI, No. 1, pp. 168–187, 9 textfigs.

FISH, CHARLES J., and JOHNSON, MARTIN W.
1937. The Biology of the Zooplankton Population in the Bay of Fundy and Gulf of Maine with Special Reference to Production and Distribution. Jour. Biol. Board Canada, Vol. 3, Ser. 3, pp. 189–322, 45 textfigs., 29 tables.

FOWLER, H. W.
1912. The Crustacea of New Jersey. Report, New Jersey State Museum, 1911 (1912), pp. 29–650, Pls. 1–150.

FRASER, C. McL.
1915. Pelagic Hydroids, in Bigelow, 1915, pp. 306–315, textfigs. 73–78.

FURRESTIN, JEAN
1938. Influence de la salinite sur la répartition du genre Sagitta dans l'Atlantique nord-est. Revue des Travaux de l'office des pêches maritimes, Vol. XI, No. 3, pp. 425-437, 6 textfigs.

GIBITZ, ANTON
1922. Verbreitung und Abstammung mariner Cladoceren. Verhandl. zool.-botan. Gesellschaft Wien. Jahrgang 1921, Vol. LXXI, pp. 85–105, 6 charts.

HARGITT, CHARLES W.
1905. The Medusae of the Woods Hole Region. Bull. U. S. Bureau of Fisheries, Vol. XXIV, 1904 (1905), pp. 21–79, pls. I-VII, textfigs.

HENSEN, VICTOR
1890. Einige Ergebnisse der Plankton-Expedition der Humboldt-Stiftung. Math. Naturwiss. Mittheil. Sitzungsbericht. König Preuss. Akad. Wiss. Berlin. Jahrgang 1890, pp. 167–177 (243–253).
1895. Methodik der Untersuchungen bei der Plankton Expedition. Ergebn. Plankton-Exped. des Humboldt-Stiftung, Vol. 1, B, 200 pp., 14 textfigs., 11 tables, 1 chart.

HJORT, JOHAN and RUUD, JOHAN T.
1938. Deep Sea Prawn Fisheries and Their Problems. Hvalrådets Skrifter, Norske Videnskaps-Akad. Oslo, No. 17, Pt. 1, pp. 1–144, 21 textfigs.

HOLMES, S. J.
1905. The Amphipoda of Southern New England. Bull. U. S. Bureau of Fisheries, Vol. XXIV, 1904 (1905), pp. 459–529, pls. I-XIII, textfigs.

HUNTSMAN, A. G.
1919. Biology of Atlantic Waters of Canada. Some Quantitative and Qualitative Plankton Studies of the Eastern Canadian Plankton. 2. On the Quantity of Plankton obtained at one hundred and seventy-nine stations during the Canadian Fisheries Expedition, 1915. Canadian Fish. Exped. 1914–1915, Depart. Naval Sci., pp. 407–420.
1919a. Biology of Atlantic Waters of Canada. Some Quantitative and Qualitative Studies of the Eastern Canadian Plankton. 3. A Special Study of the Canadian Chaetognaths, their Distribution, etc., in the Waters of the Eastern Coast. Canadian Fish. Exped. 1914–1915, Depart Naval Sci., pp. 421–485, 12 textfigs.

JESPERSEN, P.
1923. On the quantity of Macroplankton in the Mediterranean and the Atlantic. Rep. Dan. Ocean. Exped. 1908–1910 to the Mediterranean and Adjacent Seas, Vol. III, No. 7, Misc. Papers, Pt. 3, pp. 1–17, 8 textfigs.
1924. On the quantity of Macroplankton in the Mediterranean and the Atlantic. Internat. Rev. Gesamt. Hydrobiol. Hydrogr., Vol. XII, pp. 102–115.

1935. Quantitative Investigations on the Distribution of Macroplankton in Different Oceanic Regions. Dana Report, No. 7, 44 pp., 28 textfigs.

JOHNSTONE, JAMES

1908. Conditions of Life in the Sea. 332 pp., 29 figs. Cambridge, England.

KEMP, STANLEY

1938. Oceanography and the Fluctuations in the Abundance of Marine Animals. Brit. Assoc. Advance. Sci. 1938 Meet., Sect. D., Zool., pp. 85–101.

1938a. Oceanography and the Fluctuations in the Abundance of Marine Animals. Nature, Vol. 142, No. 3600, pp. 777–779.

KRAEFFT, FRITZ

1910. Über das Plankton in Ost- und Nordsee und den Verbindungsgebieten, mit besonderer Berücksichtigung der Copepoden. Wiss. Meeresuntersuch. Komm. wiss. Untersuch. deutsch. Meere, Abt. Kiel, N. F., Vol. XI, pp. 29–108, 9 textfigs., 3 tables.

LOHMAN, H.

1901. Die Appendicularien. Nordisches Plankton, Zool. Teil, Vol. II, 3, pp. 11–21, 12 textfigs.

1911. Die Appendicularien. Nachtrag. Nordisches Plankton, Zool. Teil, Vol. II, 3, pp. 23–29, 3 textfigs.

LÜCKE, FR.

1912. Quantitative Untersuchungen an dem Plankton bei dem Feuerschiff "Borkumriff" in Jahre 1910. Wiss. Meeresuntersuch. Komm. wiss. Untersuch. deutsch. Meere, Abt. Kiel, N. F., Vol. XIV, pp. 101–128, 3 textfigs., 2 tables.

MAYER, A. G.

1910. Medusae of the World. Hydromedusae. Carnegie Inst. Washington, Publ. No. 109, Vol. 1, 230 pp., 119 textfigs., 29 pls.

1912. Ctenophores of the Atlantic Coast of North America. Carnegie Inst. Washington, Publ. No. 162, 58 pp., 17 pls., 12 textfigs.

MIELCK, W.

1911. Quantitative Untersuchungen an dem Plankton der deutschen Nordsee-Terminfahrten im Februar und Mai 1906. Wiss. Meeresuntersuch. Komm. wiss. Untersuch. deutsch. Meere, Abt. Kiel, N. F., Vol. XIII, pp. 313–357.

MIELCK, W., and KÜNNE, C.

1935. Fischbrut- und Plankton-Untersuchungen auf dem Reichsforschungsdamfer "Poseidon" in der Ostsee, Mai-Juni 1931. Wiss. Meeresuntersuch. Komm. wiss. Untersuch. deutsch. Meere, Abt. Helgoland, N. F., Vol. XIX, 120 pp., 12 textfigs., 8 text-tables, 39 tables.

ORR, A. P.

1934. On the Biology of *Calanus finmarchicus*. Pt. IV. Seasonal Changes in the Weight and Chemical Composition in Loch Fyne. Jour. Mar. Biol. Assoc., U. K., N. S., Vol. XIX, pp. 613–632, 5 textfigs.

OSTENFELD, C. H., and JESPERSEN, P.

1924. Standard Net for Plankton Collections. Publ. Circ., No. 84, Cons. Perm. Int. Expl. de la Mer, 16 pp., 11 textfigs.

Parr, A. E.

1933. A geographic-ecological analysis of the seasonal changes in temperature conditions in shallow water along the Atlantic coast of the United States. Bull. Bingham Oceanogr. Collection, Vol. 4, pp. 1–90, 28 textfigs.

Ramner, Walter

1933. Die Cladoceren der "Meteor" Expedition. Wiss. Ergebn. Deutsch. Atlantisch. Exped. .... "Meteor" 1925–1927, Vol. XII, Lief. 2, pp. 111–121, textfigs. 51–52.

Ranson, Gilbert

1936. Méduses provenant des campagnes du Prince Albert I de Monaco. Res. camp. sci. Monaco, Vol. XCII, 248 pp., 2 pls.

Rathbun, Richard

1889. Notice of the small surface organisms taken in the tow-nets, and of the contents of mackerel stomachs. Bull. U. S. Fish Comm., Vol. VII, 1887 (1889), pp. 259–267.

Redfield, Alfred C.

1939. The history of a population of Limacina retroversa during its drift across the Gulf of Maine. Biol. Bull., Vol. LXXVI, No. 1, pp. 26-47, 10 textfigs.

Rosenfeld, Georg

1904. Studien über das Fett der Meeresorganismen. Wiss. Meeresuntersuch. Komm. wiss. Untersuch. deutsch. Meere, Abt. Helgoland, N. F., Vol. V, pp. 57–83.

Russell, F. S.

1925. The Vertical Distribution of Marine Macroplankton. An Observation on Diurnal Changes. Jour. Mar. Biol. Assoc., U. K., N. S., Vol. XIII, pp. 769–809, 6 textfigs.

1927. The Vertical Distribution of Marine Macroplankton. V. The Distribution of Animals Caught in the Ring-trawl in the Daytime in the Plymouth Area. Jour. Mar. Biol. Assoc., U. K., N. S., Vol. XIV, pp. 557–608, 11 textfigs., 4 tables.

1934. On the Occurrence of the Siphonophores *Muggiaea atlantica* Cunningham and *Muggiaea kochii* (Will) in the English Channel. Jour. Mar. Biol. Assoc., U. K., N. S., Vol. XIX, pp. 555–558.

1935. On the Value of Certain Plankton Animals as Indicators of Water Movements in the English Channel and North Sea. Jour. Mar. Biol. Assoc., U. K., N. S., Vol. XX, pp. 309–332, 7 textfigs.

Rudé, G. T.

1938. New methods of marine survey. Proc. Am. Phil. Soc., Vol. 79, pp. 9–25, 11 textfigs.

Savage, R. E.

1931. The Relation between the Feeding of the Herring off the East Coast of England and the Plankton of the Surrounding Waters. Fishery Invest., Min. Agri. Fish. (Great Brit.), Ser. II, Vol. XII, No. 3, 88 pp., 32 tables, 10 pls., 23 textfigs.

1937. The Food of North Sea Herring 1930–1934. Fishery Invest. Min. Agr. Fish. (Great Brit.), Ser. II, Vol. XV, No. 5, 57 pp., 16 textfigs., 29 tables.

SCHMIDT, JOHANNES

1912. Introduction. Rep. Dan. Ocean. Exped. 1908–1910 to the Mediterranean and Adjacent Seas, Vol. 1, Pt. 1, pp. 1–75, 12 textfigs.

SHARPE, RICHARD W.

1911. Notes on the marine Copepoda and Cladocera of Woods Hole and adjacent regions, including a synopsis of the genera Harpacticoida. Proc. U. S. Nat. Mus., Vol. 38, 1911, pp. 405–436, 20 textfigs.

STEPHENSEN, K.

1924. Hyperiidea-Amphipoda (Part 2, Paraphronimidae, Hyperiidae, Dairellidae, Phronimidae, Anchylomeridae). Rep. Dan. Ocean. Exped. 1908–1910 to the Mediterranean and Adjacent Seas, Vol. II, Biol., D. 4, pp. 71–149, 20 textfigs., 15 charts.

STEUER, ADOLF

1910. Planktonkunde. 723 pp., 365 textfigs., 1 pl. Leipzig and Berlin.

STØRMER, LEIF

1929. Copepods from the "Michael Sars" Expedition, 1924. Rapp. et Proc.-Verb., Cons. Perm. Int. Expl. de la Mer, Vol. LVI, 57 pp., 13 textfigs.

SUDLER, MERVIN T.

1899. The Development of Penilia schmackeri Richard. Proc. Boston Soc. Nat. Hist., Vol. XXIX, pp. 109–131, 3 pls.

SUMNER, FRANCIS B., OSBURN, RAYMOND C., and COLE, LEON J.

1913. A biological survey of the waters of Woods Hole and vicinity. Pt. II, Sect. III. A catalogue of the marine fauna of Woods Hole and vicinity. Bull. U. S. Bureau of Fisheries, Vol. XXXI, Pt. II, pp. 547–794.

THIEL, MAX EGON

1938. Die Chaetognathen-Bevölkerung des Südatlantischen Ozeans. Wiss. Ergebn. Deutsch. Atlantisch. Exped. .... "Meteor" 1925–1927, Vol. XIII, 110 pp., 62 textfigs.

WALFORD, LIONEL A.

1938. Effect of Currents on Distribution and Survival of the Eggs and Larvae of the Haddock (*Melangramus aeglefinis*) on Georges Bank. Bull. U. S. Bureau of Fisheries, Vol. XLIX, No. 29, pp. 1-75, textfigs. 1-50.

WHEELER, WILLIAM MORTON

1901. The free-swimming copepods of the Woods Hole region. Bull. U. S. Fish Comm., Vol. XIX, 1889 (1901), pp. 157–192, 30 textfigs.

WILSON, CHARLES B.

1932. The copepods of the Woods Hole region. Bull. Smithsonian Inst., U. S. Nat. Mus., 158, 635 pp., 316 textfigs., 41 pls.

1932a. The copepod crustaceans of Chesapeake Bay. Proc. U. S. Nat. Mus., Vol. 80, Art. 15, 54 pp., 5 pls.

WIMPENNY, R. S.

1929. Preliminary Observations on the Fat-Content of the Plankton on the English Herring Grounds in the North Sea. Fishery Invest. Min. Agri. Fish. (Great Brit.), Ser. II, Vol. XI, No. 5, 23 pp., 9 tables.

1937. The Distribution, Breeding and Feeding of some important Plankton Organisms of the South-West North Sea in 1934. Pt. I. *Calanus finmarchicus* (Gunn.), *Sagitta setosa* (J. Müller), and *Sagitta elegans* (Verrill). Fishery Invest. Min. Agri. Fish. (Great Brit.), Ser. II, Vol. XV, No. 3, pp. 3-53, 24 textfigs., 14 tables.

WINSOR, CHARLES P., and WALFORD, LIONEL A.
1936. Sampling Variations in the Use of Plankton Nets. Jour. Cons., Cons. Perm. Int. Expl. de la Mer, Vol. XI, No. 2, pp. 190-204, 1 textfig.

ZIMMER, CARL
1909. VI. Die nordischen Schizopoden. Nordisches Plankton, Zwölfte Lief., No. VI, 1909, pp. 1-178, 383 textfigs.

Contribution No. 195

[Reprinted from THE JOURNAL OF GENERAL PHYSIOLOGY, January 20, 1939,
Vol. 22, No. 3, pp. 391–415]

ON THE DISTRIBUTION OF VITAMINS A_1 AND A_2

BY GEORGE WALD*

(From the Biological Laboratories of Harvard University, Cambridge, and the Woods Hole Oceanographic Institution, Woods Hole†)

(Accepted for publication, October 26, 1938)

In the retinas of mammals, frogs, and certain marine fishes vitamin A participates with rhodopsin, a rose-colored photosensitive pigment of the rods, in a cycle of the form: rhodopsin $\xrightleftharpoons{\text{light}}$ retinene—protein $\longrightarrow$ vitamin A—protein $\longrightarrow$ rhodopsin (Wald, 1935–36; 1936–37; 1937–38).

In the rods of certain fresh-water fishes rhodopsin is replaced by a purple photolabile pigment which I have suggested be called *porphyropsin.* This was first observed *in situ* by Kühne and Sewall (1880), and was examined spectrographically in solution by Köttgen and Abelsdorff (1896). Porphyropsin enters a retinal cycle which is identical in form with that of rhodopsin, but contains different carotenoids in the positions of retinene and vitamin A. The substance which replaces vitamin A in the fresh-water fish retina reacts with antimony chloride to yield a deep blue color due to an absorption band at about 696 mμ, accompanied by a broad subsidiary hump at about 640 mμ (Wald, 1937).

Almost simultaneously with the announcement of these observations, Lederer and Rosanova (1937) reported that substances yielding antimony chloride bands at about 690 and 645 mμ may predominate in the liver oils of certain Russian fresh-water fishes. This observation was rapidly confirmed and extended (Edisbury, Morton, Simpkins, and Lovern, 1938; Gillam, Heilbron, Jones, and Lederer, 1938; Lederer and Rathmann, 1938). The substance responsible for the antimony chloride band at 690–697 mμ was found to possess a direct absorption band in ethanol at 345–350 mμ. It is apparently a homologue of vitamin A, possessing one added ethylenic group and the empirical formula $C_{22}H_{31}OH$ (Gillam *et al.*). A pike-perch liver oil—which I conclude from the ratio of extinctions at 693 and at 620 mμ contained little or no vitamin A—possessed growth-promoting activity in rats about equal to that of a halibut liver oil of the same Lovibond blue value (Gillam *et al.*).

---

* This research has been supported in part by a grant from the Milton Fund of Harvard University.

I am deeply indebted to Mr. J. Arthur Kitson of the Division of Fisheries and Game, Department of Conservation of the Commonwealth of Massachusetts, for gifts of live pond and hatcheries fishes; to Mr. William C. Herrington and Mr. Milton J. Lobell of the Division of Scientific Inquiry, U. S. Bureau of Fisheries for aid in procuring marine material; and to Bioproducts, Inc., Astoria, Oregon, for a shipment of Columbia River salmon livers.

† Contribution No. 195.

Since in fresh-water fishes the 696 mμ chromogen replaces vitamin A in its most specific physiological function, the synthesis of visual purple, Edisbury *et al.* (1937) have suggested that it be called vitamin A_2.[1] The retinene analogue in these fishes may similarly be called retinene$_2$. The porphyropsin cycle may then be formulated:

$$\text{Porphyropsin} \overset{\text{light}}{\rightleftharpoons} \text{retinene}_2 \dashrightarrow \text{vitamin } A_2 \dashrightarrow \text{porphyropsin.}$$

The substances heretofore called vitamin A and retinene are found exclusively in almost all vertebrates. Ordinarily it should be unambiguous to continue to refer to them without subscripts as in the past. Throughout the remainder of the present paper, however, the burden of which is a continual comparison of these substances with vitamin A_2 and retinene$_2$, I shall for greater explicitness refer to the former as vitamin A_1 and retinene$_1$ (*cf.* Lederer and Rathmann, 1938).

---

[1] In a later paper Edisbury *et al.* (1938) refer to this substance as factor A_2, apparently because "there is no evidence that its function as a vitamin extends beyond fishes." More recently Gillam *et al.* (1938) and Lederer and Rathmann (1938) appear to base the vitamin designation for A_2 principally on the demonstration of its growth-promoting activity in rats. There is some confusion in this viewpoint. The implication that the term vitamin is to be reserved to "higher" animals is equivocal, since it is already known that, for example, ascorbic acid is a vitamin in some mammals, like the guinea pig and man, and not in others, like the rat. Furthermore there is as yet no evidence that in rats A_2 acts directly, and not simply as a pro-vitamin A_1, like a number of other carotenoids. One may choose between two consistent alternatives: to restrict the term vitamin to the human accessory factors; or to apply it to all dietary accessory factors, recognizing its limitation to those animals in which its activity has been demonstrated. I believe the latter alternative to conform most closely with present usage. In this sense the 696 mμ chromogen is vitamin A_2 because it replaces vitamin A_1 in the visual systems of certain fishes.

Band maxima of the components of the rhodopsin and porphyropsin systems and of the antimony chloride reactions with their carotenoid members are listed in Table I.

No other case is known in which a vitamin appears to be restricted to a specific group of vertebrates. It is important therefore that the precise distribution of vitamins A_1 and A_2 among fishes and its significance be determined. This is the purpose of the present experiments.

TABLE I

Absorption maxima of solutions of rhodopsin and porphyropsin in aqueous digitonin, of solutions of vitamins A and retinenes in chloroform, and of antimony chloride reactions with the latter substances in chloroform.

Substance	Absorption maximum	Antimony chloride maximum
	$m\mu$	$m\mu$
Rhodopsin	500	—
Retinene$_1$	387	664
Vitamin A_1	328	615–620
Porphyropsin	522	—
Retinene$_2$	405	705
Vitamin A_2	355	696

Plan of the Research

Extracts have been examined from livers and from three eye tissues—the retina proper, the pigmented epithelium which is histologically and functionally closely bound with the neural retina, and the vascular choroid. All of these tissues but the retina proper may contain concentrations of vitamins A and other carotenoids which seem to exceed greatly their immediate needs, and probably represent temporarily inert stored material.

This is not in general true of the retina. Almost all retinal vitamin A_1 or A_2 is physiologically active, participating directly in the visual cycles. Practically all of it is consumed in the synthesis of visual purples and reappears following their exposure to light. Retinal vitamins A therefore possess a special significance; they are diagnostic of particular types of visual purple system. The retinal distribution of vitamins A ordinarily is paralleled precisely by distributions of the other components of the visual cycles, the retinenes, and rhodopsin and porphyropsin.

The observations which follow are restricted to antimony chloride reactions with the vitamins A alone for purely technical reasons: (1) the vitamins A are the only visual components common to all the tissues examined; and (2) the direct spectra of mixtures of rhodopsin and porphyropsin, of the retinenes, or of vitamins A, as shown in Table I, are separated by only about 20 mμ; in mixtures of these pigments the bands fuse to form single maxima in intermediate positions. Even the antimony chloride bands of the retinenes, 41 mμ apart, are imperfectly separated in mixtures. Only the antimony chloride maxima of the vitamins A, which are separated by 76 to 81 mμ, remain distinct in mixtures of all proportions, and permit approximate estimation of their composition by simple inspection.

The fishes which have been examined fall into four classes:

A. *Stenohaline* fishes, restricted permanently to a narrow range of salinities.

1. Permanently fresh-water fishes.
2. Permanently marine fishes.

B. *Euryhaline* fishes, capable of adult existence within a wide range of salinities.

1. Fresh-water spawners (*anadromous*).
2. Marine spawners (*catadromous*).

This classification possesses certain unusual features. It has been common practice to emphasize the *migratory* habits of certain fishes, and the terms anadromous and catadromous literally indicate migration from salt to fresh water or in the reverse direction. However, it probably is true that no fish must depart from its spawning environment to complete a normal existence. Migration to or from the sea is merely a potentiality realized in varying degree by all euryhaline fishes. The fundamental characteristic is the euryhalinity of certain adult fishes; and the added fact that this is usually combined with a very high specificity of spawning environment.

Methods

The chemical procedures employed in these experiments have intentionally been kept extremely simple, to avoid possible changes during preparation of tissues or extracts, and to facilitate eventual extension of this survey to include many more animals. Unless otherwise noted, the experiments were performed in the following manner.

Retinas were dissected in the dark in Ringer's solution immediately after each individual fish had been beheaded. They were freed from all apparent traces of pigmented epithelium and choroid, and were then exposed to bright light and left in moderate light at room temperatures for at least 1 hour to allow all retinenes formed on irradiation to be converted to vitamins A. The tissues were centrifuged, all excess fluid decanted, and were shaken vigorously by machine for about 20 minutes with benzine (petroleum ether, boiling range 30 to 60°C.). The extraction mixture was centrifuged, and the clear benzine extract decanted and evaporated to dryness under reduced pressure. The oily residue was dissolved in a small volume (usually 0.3 cc.) of dry chloroform.

After the retinas had been prepared the choroids or combined choroids and pigmented epithelia were scooped out of the sclerae into Ringer's solution and were collected by centrifuging. They were extracted by shaking with either chloroform or benzine. The extract was centrifuged clear and brought over into usually 0.3 cc. of chloroform.

Minced liver tissue was partly dehydrated by rinsing once with 95 per cent ethanol, then was digested at about 70°C. in 6 per cent potassium hydroxide in methanol. Usually after about an hour the entire tissue had gone into solution. The saponification mixture was diluted with water in stages until an equal volume had been added, and at each stage of dilution was extracted by shaking with benzine. The total benzine extract was washed repeatedly with water, and was distilled dry under reduced pressure. The oily residue was taken up in chloroform.

When not being actively worked, all preparations were stored in darkness on solid carbon dioxide.

Antimony trichloride reagent was prepared by saturating dry chloroform with fresh crystals at about 60°C. and allowing the solution to cool slowly to room temperature. Excess antimony chloride crystallizes on the sides of the container and keeps the stock solution constantly saturated at room temperatures.

Spectra were measured with the recording photoelectric spectrophotometer of Hardy (1935) at the Color Measurements Laboratory of the Massachusetts Institute of Technology. This instrument draws absorption spectra directly on graph paper, either in terms of the fraction of incident light absorbed ($1 - I/I_o$) or of the extinction or optical density, $\log I_o/I$, in which I_o is the incident and I the transmitted intensity. Fig. 8 is an original recording; all the other figures have been traced on tracing cloth from similar records. In a few instances the originals have previously been published (Wald, 1936–37).

The spectrophotometric procedure was rigidly standardized. 0.3 cc. of tissue extract in chloroform was poured into a glass cell of 3.6 cc. capacity and 10 mm. depth. This was placed in position in the spectrophotometer. 3.2 cc. of antimony chloride reagent were rapidly introduced by pipette, and recording of the spectrum began immediately. The wavelength interval from 580 to 720 mμ was negotiated in about 1 minute. During this period the initial blue test color fades slightly, but the distortion of spectrum introduced in this way is very small.

Estimation of Vitamins A_1 and A_2 in Mixtures.—Edisbury *et al.* and Gillam *et al.* have tacitly assumed that the antimony chloride bands of vitamins A_1 and A_2 do not overlap, and that their concentrations in mixtures are therefore represented directly by the extinctions at about 620 and 693 mμ respectively. Actually the bands do overlap considerably, and this way of estimating concentrations is consequently seriously misleading. It yields incorrect quantitative results, and implies the presence of both vitamins A in many oils which really contain one of them alone. I have used the following procedure for evaluating the proportions of vitamins A_1 and A_2 in mixtures.[2]

The antimony chloride bands of a number of vitamin A_1 preparations which contained no A_2, measured in the course of the present experiments, have possessed extinctions at 696 mμ 0.08 ± 0.03 of those at 618 mμ. Similarly, vitamin A_2 preparations which contained no A_1 have yielded bands possessing extinctions at 618 mμ 0.39 ± 0.04 of those at 696 mμ.

If the extinction due to vitamin A_1 at 618 mμ be x, then the extinction due to this vitamin at 696 mμ is $0.08x$. Similarly, if the extinction due to vitamin A_2 at 696 mμ is y, then that at 618 mμ due to this vitamin is $0.39y$.

$$\left.\begin{aligned}\text{Observed total extinction at 618 m}\mu &= k_{618} = x + 0.39y\\ \text{Observed total extinction at 696 m}\mu &= k_{696} = y + 0.08x\end{aligned}\right\} \qquad (1)$$

This pair of simultaneous equations reduces to the convenient form:

$$\left.\begin{aligned} x &= \frac{2.56k_{618} - k_{696}}{2.48}\\ y &= k_{696} - 0.08x\end{aligned}\right\} \qquad (2)$$

The extinction at 618 mμ due to vitamin A_1 (x) may be converted to absolute or a variety of arbitrary units by the use of appropriate factors available in the literature. Similar factors for dealing with vitamin A_2, however, have not yet been determined. I have therefore expressed the proportion of vitamins A_1 and A_2 in mixtures arbitrarily by the ratio of the extinction at 618 mμ due to vitamin A_1 to that at 696 mμ due to A_2 ($x:y$). To make such ratios conveniently comparable, as in Table II, their components have been made to sum to 100. To state this procedure somewhat differently, the computed extinctions x and y may be thought of as the respective "color equivalents" of vitamins A_1 and A_2. The sum of these extinctions may be taken as an arbitrary measure of the total vitamin A content, and the contribution to it of each vitamin expressed as a percentage of this total. An example follows.

---

[2] Recently Lederer and Rathmann (1938) have discussed and offered an approximate solution for this problem.

A chinook salmon liver oil yielded an antimony chloride spectrum with maxima at 618 and 696 mμ, and extinctions at these wavelengths of 0.428 and 0.155 respectively. Through substitution of these values in equations (2) one obtains $x = 0.379$ and $y = 0.125$. The sum of these extinctions is 0.504, of which 0.379/0.504 = 75 per cent is due to vitamin A_1 and the remaining 25 per cent to A_2.

The 618/696 mμ extinction ratios for vitamins A_1 and A_2 on which this computation is based are strictly valid only for the test and spectrophotometric procedures here employed. However, Gillam *et al.* have reported 620/697 ratios of 0.46 and 0.48 for concentrates of fresh-water fish liver oils, and 0.38 as their lowest such ratio. Lederer and Rathmann (1938) find a 620/695 ratio of 0.33 for their richest vitamin A_2 concentrates. It is clear, therefore, that the experimental techniques of these workers lead to factors comparable with that of 0.39 ± 0.04 used in the present experiments.

Observations

A. Retinas

Spectra of the antimony chloride reactions with retinal extracts from four marine teleosts are shown in Fig. 1. Those from the black sea bass, porgy, and sea robin have previously been presented as part of a study of the visual purple systems in these animals (Wald, 1936–37). Data from the sand flounder were obtained from fish killed at sea in the light adapted condition several hours before dissection of the retinas and extraction.

These fish, representing four different families, are all permanently marine forms. It is clear from Fig. 1 that their retinas contain the 615–620 mμ chromogen, vitamin A_1, and not a trace of vitamin A_2. Taxonomic notes on these fishes follow.

Black sea bass, *Centropristes striatus*. Family Serranidae, the basses. In the same family are the striped bass, which enters brackish or fresh water to spawn, and the anadromous white perch, data from which are presented below.

Porgy or scup, *Stenotomus chrysops*. Family Sparidae, the sea breams, all typically marine.

Sea robin, *Prionotus carolinus*. Family Triglidae, the gurnards, all marine.

Sand flounder, *Lophopsetta maculata*. Family Pleuronectidae, the flounders, all marine. This species is the closest North American relative of the European turbot and brill.

Similar data from the retinas of two marine elasmobranchs, the smooth and spiny dogfishes, are shown in Fig. 2 (*a*, *c*). As in the marine teleost retinas, only vitamin A_1 is present, accompanied in this instance by a trace of the 664 mμ chromogen, retinene$_1$, which has escaped conversion to the vitamin.

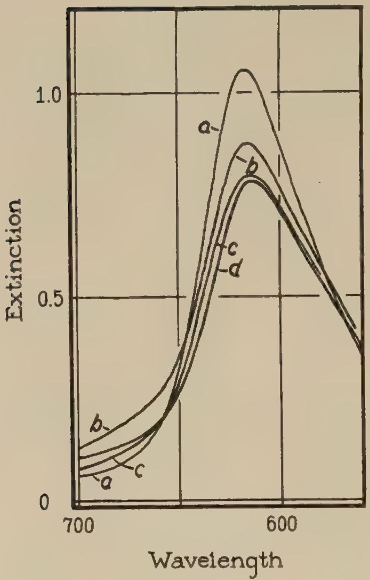


FIG. 1

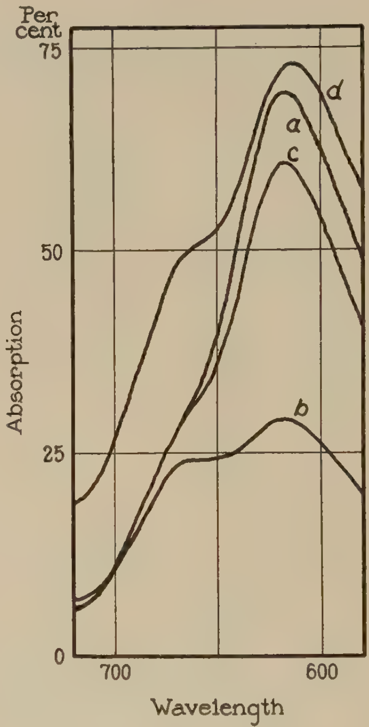


FIG. 2

FIG. 1. Marine teleost retinas. Spectra of the antimony chloride reaction with total benzine extracts of (*a*) two sea bass, (*b*) five scup, (*c*) two sand flounder, and (*d*) five sea robin retinas. These tissues contain the 618 mμ chromogen vitamin A_1 alone.

FIG. 2. Marine elasmobranch eye tissues. Antimony chloride reaction with total benzine extracts of (*a*) four retinas and (*b*) eight choroids of smooth dogfish; and (*c*) six retinas, and (*d*) twelve choroids of spiny dogfish. These tissues contain only vitamin A_1, accompanied by small quantities of the 664 mμ chromogen, retinene$_1$.

The experiments which follow afford strong evidence that the retinal vitamin A configuration is correlated primarily with the environment in which the fish is spawned. It is interesting, therefore, that both these dogfishes are viviparous. Their taxonomic positions are noted below.

Smooth dogfish (Bigelow and Welsh: *Galeorhinus laevis*; Jordan and Evermann: *Mustelus canis*). Family Galeorhinidae, the smooth dogfishes.

Spiny dogfish, *Squalus acanthias*. Family Squalidae, the spiny dogfishes.

Precisely the same procedures as show the presence of vitamin A_1 alone in the retinas of these marine fishes yield an entirely different result when applied to typically fresh-water forms. Spectra of the antimony chloride reaction with retinal extracts from one anadromous and three permanently fresh-water fishes are shown in Fig. 3. No trace of the vitamin A_1 band appears in any of these spectra. Instead they are dominated by the high band at 696 mμ specific for vitamin A_2. A low hump centering at 640 to 645 mμ accompanies the vitamin A_2 band in varying proportions; it possibly is due to some other carotenoid, as yet unidentified.[3]

The carp, calico bass, and pickerel represent three families, all of whose members permanently inhabit fresh water. The white perch, however, though it spawns in fresh water, is indifferent in its adult environment. The individuals used in the present experiments were caught in a fresh-water stream in May. Since this is the spawning season, they may have come up from the sea or equally well may have spent their entire lives in fresh water.

The retina of the white perch contains vitamin A_2 alone, while that of its close marine relative, the black sea bass, contains only vitamin

---

[3] Vitamin A_1 preparations usually possess in addition to direct absorption at 328 mμ and an antimony chloride band at about 620 mμ, subsidiary absorption at about 270 mμ and a second antimony chloride maximum at about 580 mμ. The latter properties appear to be due to a distinct substance, hepaxanthin (von Euler, Karrer, and Zubrys, 1934). Similarly vitamin A_2 possesses a satellitic direct absorption at about 290 mμ and antimony chloride maximum at 640-650 mμ. Edisbury *et al.* (1938) have reported the separation of a vitamin A_2 preparation into fractions possessing direct absorptions at 350 mμ and predominantly at 285–290 mμ. Lederer and Rathmann (1938), however, have failed to confirm this observation and believe both bands probably due to vitamin A_2 itself.

A_1. However, the remaining eye tissues of the white perch contain both vitamins A in about equal proportions, while in the permanently fresh-water species examined they possess vitamin A_2 alone (see below). Consequently, in vitamin A configuration as well as in salinity relations, the white perch is distinct from all the other fishes so far mentioned. It is most like the permanently fresh-water forms, as though correlated with its fresh-water origin; and shares slightly the marine type vitamin A_1, as though associated with its euryhalinity.

This group of fishes may be divided also on a nutritional basis, since the carp is characteristically vegetarian, the other forms carnivorous. Apparently this difference in habit does not affect the retinal vitamin A configuration.

Taxonomic notes on these fishes follow.

Pickerel, *Esox reticulatus*. Family Esocidae, the pikes, all permanently fresh-water.

Calico bass, *Pomoxis sparoides*. Family Centrarchidae, the sunfishes, all permanently fresh-water.

Carp, *Cyprinus carpio*. Family Cyprinidae, the carps and minnows. This is the most extensive family of fresh-water fishes.

White perch, *Morone americana*. Family Serranidae, the basses.

Probably the most prominent of euryhaline fishes are the anadromous salmonids, which run the gamut from the potentially to the habitually migratory; and the catadromous eel.

It is now well known from the work of Schmidt (1924) that the American fresh-water eel is spawned in the Sargasso Sea (Lat. 20–30° N., Long. 60–80°W.). The larvae migrate northward along our shores, metamorphose to elvers in the sea when about 1 year old, and at the age of 15 to 16 months ascend the rivers and streams into fresh water. The eel commonly spends the subsequent 5 to 20 years in fresh water before returning to the sea to spawn.

The chinook or king salmon performs the reverse migration. It is spawned in fresh water, and the young parr spend from several months to 2 years in this environment before descending to the sea. Adolescent or precocious individuals may thereafter reappear in fresh water in their second or third years (grilse). The mature salmon return to fresh water to spawn principally in the fourth and fifth and as late as the seventh years (Gilbert, 1912).

It is important to note that though this is the usual history, many generations of chinook and other salmons have lived permanently in inland fresh-water ponds without detriment; and it is very probable similarly that many so called fresh-water eels never leave the sea.

Brook and rainbow trout, which also are salmonids, both spawn in fresh water and are indifferent in their adult habitats. Rainbow trout rarely leave fresh water, but sea-running brook trout (sea trout) are relatively common. These three salmonids therefore typify anadromous migration in all degrees of realization.

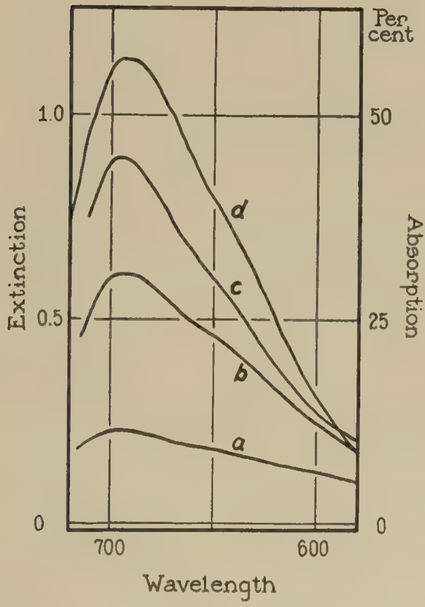


FIG. 3

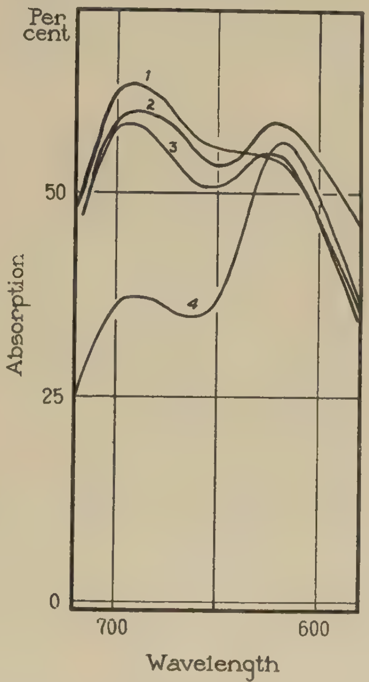


FIG. 4

FIG. 3. Fresh-water teleost retinas. Antimony chloride reaction with total benzine extracts of (*a*) eight pickerel, (*b*) eight calico bass, (*c*) six white perch retinas, and (*d*) one carp retina. Ordinates for curves *a* to *c* are extinction, for *d* percentage absorption. These tissues contain only vitamin A_2, accompanied by traces of the unidentified 645 mμ chromogen.

FIG. 4. Retinas of euryhaline fishes. Antimony chloride reaction with total benzine extracts of groups of seven retinas from (1) chinook salmon, (2) rainbow trout, (3) brook trout, and (4) eels. All of these tissues contain mixtures of vitamins A_1 and A_2, the anadromous salmonids a predominance of the latter, and the catadromous eel a predominance of the former.

Antimony chloride reactions with retinal extracts from these fishes and the eel are shown in Fig. 4. All four spectra show clearly the presence of mixtures of both vitamins A_1 and A_2, the eel predominantly the former and the salmonids predominantly the latter. The accurate proportions of the vitamins A, computed as described above, are presented in Table II. They show a much greater predominance of A_2 over A_1 in the salmonids than is apparent on inspection of the figure.

The eels which have been examined were mature females, caught either in fresh water or in salt marshes along the coast at the start of their spawning migration. No significant differences in vitamin A distribution are associated with these differences in habitat. These fish had experienced both marine and fresh-water existence, and the presence in the retina of both vitamins A might be a supposed consequence of this duality of environment. In any case the vitamin A pattern, once established, appears to be permanent, since the eel retains primarily marine type vitamin A_1 after years of existence in fresh water.

The trout and salmonids used in these experiments were obtained from a hatchery, and had not at any time been exposed to salt water. Nevertheless their retinas contain considerable quantities of vitamin A_1. These animals of known life history demonstrate a relation which probably is valid for all the euryhaline fishes examined; the presence of both vitamins A in the eye tissues precedes and is independent of duality of environment. It is a genetic property of the species, not a physiological consequence of migration.

The retinas of the euryhaline eel and salmonids possess predominantly the vitamin A ordinarily associated with the environment in which each is spawned. This is accompanied secondarily by the alternative vitamin A, as though correlated with their potentiality for life in both salt and fresh water, whether or not this potentiality has been realized.[4]

---

[4] The observation that the vitamin A pattern is correlated primarily with the spawning environment of these fishes is consistent with the judgment of a number of naturalists on their nature. Schmidt (1924) writes of the eel, "The Anguilla species, in contrast to other muraenoids, are usually termed fresh-water eels, and are reckoned among the fresh-water fishes of Europe and North America. From what we have now learned this is far from literally strict. Both from their history

Taxonomic data for these fishes follow.

Eel, *Anguilla rostrata.* Family Anguillidae, the true eels.

The following are members of the family Salmonidae, which includes the whitefishes, salmons, and trouts, all anadromous or fresh-water fishes:

Brook trout, *Salvelinus fontinalis.*

Rainbow trout, *Salmo irideus.* Among the American salmonids, this most nearly resembles the European *Salmo fario.*

Chinook, king or Columbia River salmon, *Oncorhynchus tschawytscha.*

B. Combined Retina and Pigmented Epithelium

All the foregoing experiments except that upon the sand flounder were performed with fresh isolated dark adapted retinas prepared in the laboratory. The experiments now to be reported, with one exception, concern fishes obtained several hours after death in a light adapted condition. In this state the pigmented epithelium ordinarily adheres firmly to the retina. In the tautog alone of all the fishes examined the same condition is found in the dark adapted eye; in this instance the freshly dissected retinas and pigmented epithelia were irradiated as were the isolated retinas in the preceding section. In all these cases benzine extracts of the combined tissues were prepared in the usual manner. Their antimony chloride reactions are shown in Fig. 5. These results are to be interpreted with a specific caution. It is possible in this type of experiment for vitamins A from the pigmented epithelium to "swamp" those from the retina, so that small amounts of one or the other vitamin A which might have appeared in extracts of isolated retinas might not be demonstrable in extracts of the combined tissues.

---

and their actual manner of life, these "fresh-water eels" are true oceanic fishes, and the remarkable point in their life history is not so much the fact of their migrating out into the sea to spawn as in their leaving it in order to pass their period of growth in an environment so unusual for muraenoid fishes as fresh water." Concerning the Atlantic salmon, Goode (1903, p. 445) comments, "I am inclined to the view that the natural habitat of the Salmon is in the fresh waters, the more so since there are so many instances—such as that of the Stormontfield Ponds in England—where it has been confined for years in lakes without apparent detriment." "That the chinook salmon has been kept for years in fresh water ponds in France is another strong evidence of the correctness of this view" (Jordan and Evermann, 1902).

The marine haddock, whiting, and herring eye tissues all contain vitamin A_1 alone. The herring forms with the alewife a pair similar to the sea bass and white perch. The former fish belong to one family and resemble each other closely anatomically. The herring is permanently marine, but the alewife enters fresh water to spawn. Immediately afterward it returns to the sea; and since the young fry migrate seaward within several months after hatching, ordinarily this fish spends only a few months of its entire existence in fresh water. Still its eye contains predominantly, perhaps exclusively, the fresh-water fish type vitamin A_2. This is a striking added demonstration that the vitamin A configuration of the eye tissues is principally and permanently associated with the spawning environment.[5]

The data so far presented reveal so precise a correlation between vitamin A distribution and salinity relations as to sharply accentuate the case of the tautog. The tautog alone of all the fishes examined possesses a vitamin A pattern the reverse of that found generally.

The combined retinas and pigmented epithelia of several dark adapted tautogs were extracted *in darkness* three times with benzine in order to remove stored vitamins A and permit the retinal changes following irradiation to be estimated. The first two extracts contained a moderate quantity of vitamin A_2, the third only a faint trace of this vitamin. The tissue was exposed to bright light and left in moderate light at room temperature for about 1½ hours. A fourth benzine extract now yielded curve *e* of Fig. 5. It shows the formation, during bleaching, of a large quantity of new vitamin A_2 accompanied by a small amount of A_1. Similar results have been obtained previously only from anadromous fishes. Yet the tautog is permanently marine, as are also all members of its family, the Labridae. The possible significance of this situation is discussed below. Taxonomic data on the fishes just reviewed follow.

Haddock, *Melanogrammus aeglifinus*. Family Gadidae, the cods.

Whiting or silver hake, *Merlucius bilinearis*. Family Merlucidae, the silver hakes.

---

[5] The alewife, like the salmonids and white perch, may spend its entire existence in fresh water without detriment. Large numbers are found, apparently land-locked, in Lake Ontario and certain small lakes in New York State (Jordan and Evermann, 1902).

The sea herring, *Clupea harengus*, and the alewife, *Pomolobus pseudoharengus*, are members of the same family, the Clupeidae.

Tautog, *Tautoga onitis*. Family Labridae, the cunners or wrassefishes.

C. *Choroid and Pigmented Epithelium*

The pigmented layers of all the marine fishes examined contain vitamin A_1 alone. Data from the herring and sand flounder are shown in Fig. 6 (*c*, *d*), and from the smooth and spiny dogfishes in Fig. 2 (*b*, *d*). The latter display small amounts of the 664 mμ chromogen, retinene$_1$. This substance has not previously been found in the pigmented layers, and its significance in this situation in the dogfishes is problematical.

Antimony chloride tests with pigmented layer extracts from the fresh water carp and calico bass are shown in Fig. 6 (*a*, *b*). They reveal no trace of vitamin A_1, but instead high concentrations of A_2, accompanied by the unknown 645 mμ chromogen. The latter is more prominent in these extracts than in the retinal oils.

Similar tests with extracts from euryhaline fishes are shown in Fig. 7. Curves *a*, *b*, and *c* from the salmonids demonstrate mixtures of vitamins A_1 and A_2 with a clear predominance of the latter. Curve *d*, from the eel, also displays the bands of both vitamins A, apparently in reverse proportion to the salmonids. The computed proportions of vitamins A in all these extracts are presented in Table II; they show the "color equivalents" of A_1 and A_2 to be about equal in the eel tissues.

White perch pigmented layers yield a peculiar result (Fig. 7*e*). The test spectrum is dominated by the 645 mμ band which heretofore has appeared only as a faint satellite of the 696 mμ absorption. Low bands due to vitamins A_1 and A_2 may also be distinguished, but their proportions cannot be estimated in this preparation. A similar result has been obtained by Edisbury *et al.* (1938) with a liver oil from the true perch (*Perca fluviatilis*).

The pigmented layers, therefore, present about as precise correlation of vitamin A pattern with salinity relations as do the retinas. This observation lessens the force of our distinction between the retina proper, practically all of whose vitamins A are directly involved in the visual processes, and the extra-retinal tissues in which vitamins A seem merely to be stored. Apparently the accumulation of vitamins

A may be a highly selective process even in tissues which contain much larger amounts than they appear to utilize. The vitamin A

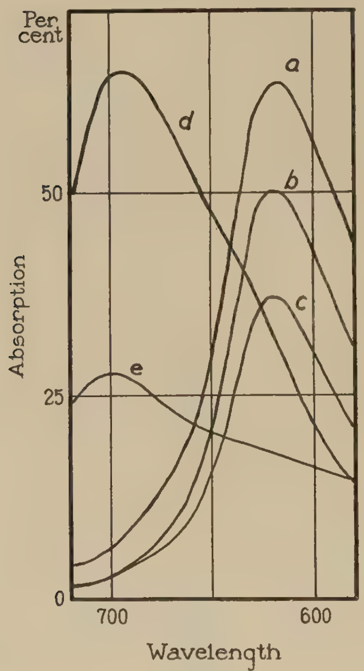


FIG. 5

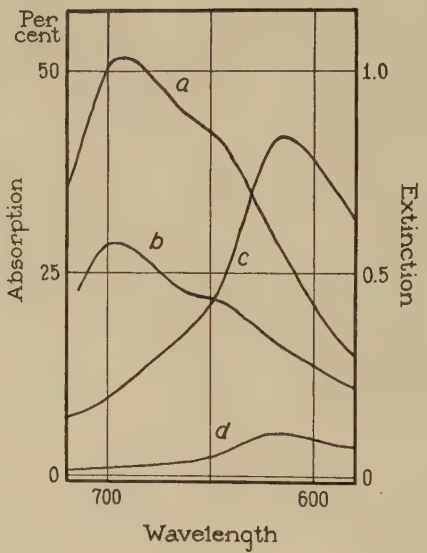


FIG. 6

FIG. 5. Combined retinas and pigmented epithelia. Antimony chloride reactions with benzine extracts from the marine (*a*) herring, (*b*) whiting, (*c*) haddock, and (*e*) tautog; and (*d*) from the anadromous alewife. The predominance of vitamin A_2 in the tautog tissues is the reverse of the results obtained with all the other marine fishes examined.

FIG. 6. Pigmented epithelia and choroids of stenohaline fishes. Antimony chloride reactions with chloroform extracts of the combined tissues from (*a*) four carp, (*b*) eight calico bass, (*c*) one sand flounder; and (*d*) of the choroids from seven herring. Ordinates of curves *a*, *c*, and *d* are per cent absorbed, for *b* are extinction. Tissues from the marine fishes contain vitamin A_1 alone, those from the fresh-water fishes only vitamin A_2.

configuration not only of the retina but of all the tissues of the ocular fundus is a genetic characteristic, primarily independent of the immediate environment and life history of the fishes examined.

D. Liver

The vitamin A pattern and salinity relations are not correlated as precisely in the liver as in the eye tissues. Most liver oils contain mixtures of both vitamins A, occasionally in proportions the reverse of those in the eye. The relative amounts of vitamins A_1 and A_2 in fish livers, computed as described above, are presented in the last two columns of Table II. Similar data on the liver oils of a large number of European fishes appear in the papers of Edisbury *et al.* (1938), Gillam *et al.* (1938), and Lederer and Rathmann (1938).

TABLE II

Proportions of vitamins A_1 and A_2 in fish eye tissues and livers. These are stated in terms of "color equivalents:" the extinction at 618 $m\mu$ due to vitamin A_1, compared with the extinction at 696 $m\mu$ due to vitamin A_2. Each pair of values is summed to 100, so that each figure has the force of a percentage.

Type	Fish	Retinas		Other eye tissues		Livers	
		A_1	A_2	A_1	A_2	A_1	A_2
Marine	Sea bass	100	0	—	—	—	—
	Scup	100	0	—	—	—	—
	Sea robin	100	0	—	—	—	—
	Sand flounder	100	0	100	0	94	6
	Smooth dogfish	100	0	100	0	—	—
	Spiny dogfish	100	0	100	0	100	0
	Herring	100*	0	100	0	80	20
	Haddock	100*	0	—	—	—	—
	Whiting	100*	0	—	—	—	—
	Tautog	18*	82	—	—	—	—
	Halibut	—	—	—	—	92	8
	Cod	—	—	—	—	100	0
Fresh water	Pickerel	0	100	—	—	0	100
	Calico bass	0	100	0	100	0	100
	Carp	0	100	0	100	65–75	25–35
Anadromous	White perch	0	100	?	?	—	—
	Alewife	0*	100	—	—	19	81
	Chinook salmon	29	71	20	80	75–80	20–25
	Rainbow trout	38	62	30	70	41	59
	Brook trout	35	65	30	70	90	10
Catadromous	Eel	62	38	50	50	99	1

* Pigmented epithelium included.

All the marine fish livers here examined contain a marked predominance of vitamin A_1, but the sand flounder and herring, which possess this vitamin exclusively in the eye, contain in addition vitamin A_2 in the liver oils. Similarly the halibut liver, in which the presence of a 690–695 mμ chromogen was first reported (Heilbron *et al.*, 1931), contains about $\frac{1}{10}$ as much vitamin A_2 as A_1.

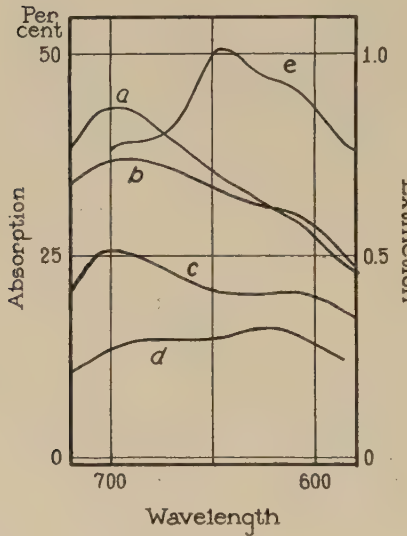


FIG. 7

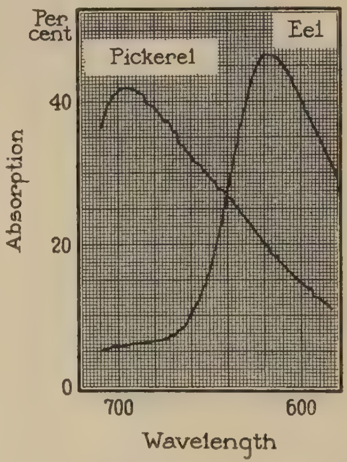


FIG. 8

FIG. 7. Combined pigmented epithelia and choroids of euryhaline fishes. Antimony chloride reactions with chloroform extracts from (*a*) seven chinook salmon, (*b*) seven rainbow trout, (*c*) seven brook trout, (*d*) seven eels, and (*e*) with a benzine extract from six white perch. All these tissues contain mixtures of vitamins A_1 and A_2, and, with the possible exception of the white perch, predominantly the vitamin A ordinarily associated with the spawning environment. Ordinates for curve *e* are extinctions, for all the other curves percentages absorbed.

FIG. 8. Antimony chloride reactions with liver oils from pickerel and eels caught in the same inland fresh-water pond. The pickerel liver contains vitamin A_2 alone, the eel about 99 per cent vitamin A_1. The curves are original photoelectric recordings.

The fresh-water pickerel and calico bass livers contain vitamin A_2 exclusively, as do their eye tissues. The carp, however, which possesses only vitamin A_2 in its eye, contains predominantly vitamin A_1 in its liver.

The livers of all the anadromous fishes examined contain mixtures of both vitamins A. The proportions in the alewife and rainbow trout are like those in the eyes, while in the chinook salmon and brook trout these proportions are reversed.

The catadromous eel contains almost exclusively vitamin A_1 in its liver. It is more "marine" in this respect than many of the permanently marine fishes, and this property is unaltered by years of fresh-water existence. It is significant that the eel, pickerel, and calico bass liver data in Table II were derived from fishes all caught in the same inland fresh-water pond, where they had shared the same environment and presumably largely the same food. Yet the proportions of vitamins A in the eel liver are almost diametrically the opposite of those in the permanently fresh-water forms. This relation is demonstrated very strikingly in Fig. 8. It is clear that the vitamin A configuration of the liver, like that of the eye, is determined by genetic and not by environmental factors.

This conclusion is confirmed in an observation on chinook salmon livers. Those which yielded the data in Table II were obtained from yearling hatcheries fish which had never left fresh water. Similar extracts have been prepared from livers of adult fishes, caught at the mouth of the Columbia River at the beginning of their spawning migration. The proportion of vitamin A_1 to A_2 found in these mature fish was as 88 to 12, not seriously different from that in the fresh water parr.

It may be concluded, therefore, that though the vitamin A pattern of the liver is not correlated as closely as that of the eye with the salinity type, it is equally independent of environmental fluctuation and is to an equal degree a racial characteristic.[6]

---

[6] This conclusion should apply strictly only to what may be termed endogenous vitamin A, that is, vitamin A synthesized by the organism itself from carotenoid precursors. Lederer and Rathmann (1938) have shown that rats and frogs, the livers of which normally contain little or no vitamin A_2, can accumulate this vitamin when fed fresh-water fish liver concentrates. It is probable that by similar means the vitamin A configuration in the liver of any animal might be displaced in either direction.

DISCUSSION

The observations reported above permit a tentative statement of the significance of the vitamin A pattern of eye and liver oils in fishes. This is best introduced by a recapitulation of the argument dispersed throughout the foregoing pages.

The eye tissues of all marine fishes examined except the tautog contain exclusively vitamin A_1; those of all the fresh-water fishes contain only vitamin A_2; those of all euryhaline fishes, with the possible exception of the alewife, possess mixtures of both vitamins, and always predominantly that one which ordinarily is associated with the spawning environment. The liver oils in general share these relations imperfectly; usually they contain mixtures of both vitamins A, occasionally in reverse proportions to the eye tissues. These observations are summarized numerically in Table II.

The vitamin A configuration might be determined by the environment of the embryo, or of the mature fish, or it might be genetic in origin.

I. The vitamin A pattern is not determined by the spawning environment, though highly correlated with it.

a. Viviparous dogfishes possess vitamin A_1 alone, like many oviparous marine fishes.

b. The eyes and livers of euryhaline fishes contain both vitamins, though each species spawns in either fresh water or in the sea.

c. Tautog eye tissues contain predominantly vitamin A_2, though this fish spawns in the sea.

II. The vitamin A pattern is not determined by the salinity of the adult environment.

a. Salmonids which have never left fresh water still possess both vitamins A. Their proportions in chinook salmon livers are essentially the same in yearling fresh-water fish and in mature animals just in from the ocean.

b. The eel retains a great predominance of vitamin A_1 after years of existence in fresh water, the alewife a predominance of A_2 after years in the sea.

c. The eye tissues of mature marine tautogs contain primarily vitamin A_2.

III. The vitamin A pattern is not determined by nutrition.

a. The vegetarian carp possesses the same pattern in its eye tissues as the carnivorous pickerel and calico bass.

b. Conversely, eels caught in the same pond as pickerel and calico bass, and presumably sharing the same food, possess the reverse type of vitamin A pattern.

c. Eels caught in salt marshes at the beginning of their spawning migration seaward possess empty digestive tracts, having apparently ceased to feed. After being kept subsequently in fresh water without food for an additional 4 months, they possess the same eye and liver vitamin A patterns as eels freshly caught in an inland pond.

I conclude that the vitamin A configurations of both eye and liver are determined by genetic factors. Presumably these operate through specific enzyme systems which govern the conversion of dietary carotenoids, ultimately of plant origin, into the vitamins A.

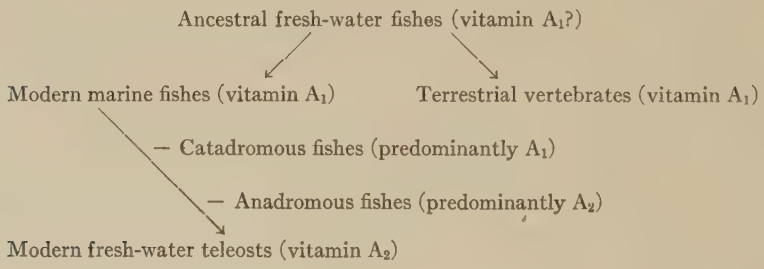
The conditions of steno- and euryhalinity and the choice of spawning environment are also inherited. We have to deal therefore with the correlation of two types of genetic character rather than with some labile functional relation. The significance of this correlation is to be sought in the phylogeny rather than in the physiology of the fishes.

Considerable anatomical and paleontological evidence indicates that all fishes originated in fresh water (Smith,1932). The ancestors of modern marine forms appear to have migrated to the sea principally in late Paleozoic and early Mesozoic times (Romer and Grove, 1935). The modern fresh-water fishes, however, may be divided into two groups: (1) those like the lung fishes which probably have continuously occupied fresh-water environments; none of these has yet been included in the present research; and (2) the modern fresh-water teleosts, which, it is generally agreed, have re-entered fresh water from the sea. In this sense the fresh-water teleosts are secondarily derived from the marine teleosts, and so represent the most recent general evolutionary development among the fishes.[7]

The connection between this development and the distribution of vitamins A may be formulated tentatively as follows. The ancestral fresh-water fishes probably possessed vitamin A_1 alone, and communicated this to both their marine and terrestrial descendants. This is therefore the vitamin A almost universal among the vertebrates. It may still be retained by the continuously fresh-water line of lung fishes. In the modern teleosts two evolutionary trends emerge: re-migration to fresh water, and assumption of vitamin A_2 metabolism. Considering only the eye tissues, the stenohaline marine fishes, with few exceptions, have retained exclusively vitamin A_1. The stenohaline fresh-water forms have negotiated completely both migration and the transfer to vitamin A_2. The euryhaline fishes, which may be regarded as transitional in the migratory sense, possess intermediate mixtures of both vitamins A. If the anadromous alewife, white perch, and salmonids may be considered to be further advanced in their evolutionary migration to fresh water than the catadromous eel, even these distinctions are reflected faithfully in the vitamin A patterns (see diagram). The correlation between both these evolutionary developments is well nigh complete. Yet apparently one may occur without the other, since the tautog has developed a predominantly vitamin A_2 visual system without to our knowledge ever having left the sea.

---

[7] I am greatly indebted to Professor A. S. Romer of Harvard University for a critical discussion of the phylogeny of the fishes.


Ancestral fresh-water fishes (vitamin A_1?)
Modern marine fishes (vitamin A_1)
Terrestrial vertebrates (vitamin A_1)
Catadromous fishes (predominantly A_1)
Anadromous fishes (predominantly A_2)
Modern fresh-water teleosts (vitamin A_2)

This situation offers a comparatively recent parallel to the alteration in muscle phosphagens associated with the origin of the vertebrates. Almost all invertebrate muscles possess arginine phosphate alone; an echinoderm (*Strongylocentrotus*) and a primitive chordate (*Balanoglossus*), both believed by some paleontologists to represent intermediate types in the progression from invertebrates to vertebrates, possess mixtures of arginine and creatine phosphates; and *Amphioxus* and the vertebrates possess creatine phosphate alone (Meyerhof, 1930[8]; Needham, Needham, Baldwin, and Yudkin, 1932).

---

[8] P. 93.

Perhaps also comparable with the vitamin A situation is the synthesis in certain fishes of trimethyl amine oxide. Hoppe-Seyler and Schmidt (1927) have found this product in all marine fishes examined, but not a trace of it in fresh-water forms. It is significant, however, that among the latter the authors include the Atlantic salmon and the European fresh-water eel. This property therefore does not appear to be intermediate in the euryhaline fishes, and may, as the authors suggest, be a direct environmental response.

There is no evidence that any of these biochemical changes constitutes an evolutionary advantage. The substitution of creatine for arginine, trimethyl amine oxide for other nitrogenous end-products, or vitamin A_2 for A_1 entails no obvious increase in fitness. On the other hand the change from sea to fresh water or the assumption of a notochord are not similarly indifferent. It is probably because they are genetically bound to such highly selective changes that these relatively neutral biochemical developments are perpetuated.

SUMMARY

The distribution of vitamins A_1 and A_2 has been determined in the eye tissues and livers of a number of fishes. The vitamins were differentiated by means of the antimony chloride reaction, which yields with A_1 a band at 615–620 mμ and with A_2 a band at about 696 mμ. In the retina the presence of vitamin A_1 is diagnostic of the operation of a rhodopsin, and vitamin A_2 of a porphyropsin cycle.

The eye tissues of all permanently marine fishes examined, except the tautog, contain vitamin A_1 alone. Those of all permanently fresh-water fishes possess only vitamin A_2. Those of all euryhaline (potentially migratory) fishes, except possibly the alewife, contain mixtures of both vitamins A, and always predominantly that one which ordinarily is associated with the environment in which the fish is spawned.

These correlations extend in part to the liver oils, but most livers contain mixtures of both vitamins A, and occasionally in proportions the reverse of those in the eye tissues.

The vitamin A configuration does not depend upon environmental circumstances, but is determined genetically. The transfer from vitamin A_1 to A_2 metabolism appears associated phylogenetically with migration of marine teleosts into fresh water.

REFERENCES

Bigelow, H. B., and Welsh, W. W., Fishes of the Gulf of Maine, *Bull. Bureau Fisheries*, 1925, **40,** pt. 1.

Edisbury, J. R., Morton, R. A., and Simpkins, G. W., A possible vitamin A_2, *Nature*, 1937, **140,** 234.

Edisbury, J. R., Morton, R. A., Simpkins, G. W., and Lovern, J. A., The distribution of vitamin A and factor A_2, *Biochem. J.*, London, 1938, **32,** 118.

von Euler, H., Karrer, P., and Zubrys, A., Wachstumsversuche mit Carotinoiden, *Helv. Chim. Acta*, 1934, **17,** 24.

Gilbert, C. H., Age at maturity of the Pacific Coast salmon of the genus Oncorhynchus, *Bull. Bureau Fisheries*, 1912, **32,** Doc. No. 767.

Gillam, A. E., Heilbron, I. M., Jones, W. E., and Lederer, E., On the occurrence and constitution of the 693 mμ chromogen (vitamin A_2?) of fish liver oils, *Biochem. J.*, London, 1938, **32,** 405.

Goode, G. B., American fishes, Boston, L. C. Page and Co., 1903.

Hardy, A. C., A new recording spectrophotometer, *J. Opt. Soc. America*, 1935, **25,** 305.

Heilbron, I. M., Gillam, A. E., and Morton, R. A., Specificity in tests for vitamin A. A new conception of the chromogenic constituents of fresh and aged liver oils, *Biochem. J.*, London, 1931, **25,** 1352.

Hoppe-Seyler, F. A., and Schmidt, W., Ueber das Vorkommen von Trimethylaminoxyd, *Z. Biol.*, Berlin, 1927, **87,** 59.

Jordan, D. S., and Evermann, B. W., American food and game fishes, New York, Doubleday, Page and Co., 1902.

Köttgen, E., and Abelsdorff, G., Absorption und Zersetzung des Sehpurpurs bei den Wirbeltieren, *Z. Psychol. u. Physiol. Sinnesorgane*, 1896, **12,** 161.

Kühne, W., and Sewall, H., Zur Physiologie des Sehepithels, insbesondere der Fische, *Untersuch. physiol. Inst. Univ. Heidelberg*, 1880, **3,** 221.

Lederer, E., and Rathmann, F. H., A physico-chemical and biochemical study of vitamin A_2, *Biochem. J.*, London, 1938, **32,** 1252.

Lederer, E., and Rosanova, W., Studies on vitamin of fish liver oils. I. An abnormal reaction of Carr and Price, *Biochimia*, 1937, **2,** 293.

Meyerhof, O., Chemische Vorgänge im Muskel, Berlin, J. Springer, 1930.

Needham, D. M., Needham, J., Baldwin, E., and Yudkin, J., A comparative study of the phosphagens, with some remarks on the origin of vertebrates, *Proc. Roy. Soc. London, Series B*, 1932, **110,** 260.

Romer, A. S., and Grove, B. H., Environment of the early vertebrates, *Am. Midland Nat.*, 1935, **16,** 805.

Schmidt, J., The breeding places of the eel, *Ann. Rep. Smithsonian Inst.*, 1924, 279.

Smith, H. W., Water regulation and its evolution in the fishes, *Quart. Rev. Biol.*, 1932, **7,** 1.

Wald, G., Vitamin A in eye tissues, *J. Gen. Physiol.*, 1934–35, **18,** 905.

Wald, G., Carotenoids and the visual cycle, *J. Gen. Physiol.*, 1935–36, **19,** 351.

Wald, G., Pigments of the retina. I. The bullfrog, *J. Gen. Physiol.*, 1935–36, **19,** 781.

Wald, G., Pigments of the retina. II. The sea robin, sea bass, and scup, *J. Gen. Physiol.*, 1936–37, **20,** 45.

Wald, G., On rhodopsin in solution, *J. Gen. Physiol.*, 1937–38, **21,** 795.

Wald, G., Visual purple system in fresh-water fishes, Nature, 1937, **139,** 1017.

Contribution No. 196

Reprinted from Biological Bulletin, Vol. LXXVI, No. 1, 26–47, Feb., 1939
Printed in U. S. A.

THE HISTORY OF A POPULATION OF LIMACINA RETROVERSA DURING ITS DRIFT ACROSS THE GULF OF MAINE

ALFRED C. REDFIELD

(From the Biological Laboratories, Harvard University, and the Woods Hole Oceanographic Institution, Woods Hole, Mass.)

THE HISTORY OF A POPULATION OF LIMACINA RETROVERSA DURING ITS DRIFT ACROSS THE GULF OF MAINE

ALFRED C. REDFIELD

(*From the Biological Laboratories, Harvard University, and the Woods Hole Oceanographic Institution,*[1] *Woods Hole, Mass.*)

Geographical distribution in the sea is a hydrodynamic problem, in which the flow of waters determines not only the "climate" of specific regions, but also the supply of organisms to populate these regions. A pelagic population must drift with the waters in which it lives. In contrast to littoral and terrestrial populations, there is no inherent fixity in its occurrence, save that determined by the current systems of the sea. The continuous drift of water through a given region not only raises questions regarding the maintenance of a population there (Damas, 1905; Sømme, 1933, 1934); it renders continuous observation on the natural history of the population singularly difficult, since the individuals observed at any place one day are different from those observed at the same place on another occasion.

Immigrant plankton which do not thrive or reproduce in the Gulf of Maine, but which are carried into its waters from offshore, were found by Bigelow (1926) to occur in a zone extending from the Eastern Channel along the eastern, northern and western sectors of the Gulf as though carried thither by the great cyclonic eddy which Huntsman (1924) and Bigelow (1927) have shown to dominate the circulation of the Gulf. Animals of arctic origin, *Limacina helicina, Mertensia ovum, Oikopleura van hoffeni,* and *Ptychogena lactea* were taken only in the eastern sector of this zone, apparently being unable to survive long enough to be borne further. Other immigrants, both of boreal and tropical origin, survived until carried as far as the offing of Cape Cod, but few were ever taken in the southern sector of the circuit. As his cruises were not taken with sufficient frequency, these observations yield no evidence concerning the velocity of the drift on which these invaders were borne, although its course was clearly enough indicated.

The observations on the pteropod *Limacina retroversa* Fleming[2] described in this paper are of interest because during the greater part of the year it has been possible to follow the history of a rather definite population as it drifted across the Gulf of Maine, noting its rate of spread, its mortality, the growth and reproduction of its individuals, and its replacement by another population of the same species.

---

[1] Contribution No. 196 from the Woods Hole Oceanographic Institution.

[2] We have employed the name *Limacina retroversa* Fleming because of its current use in oceanography. Dr. W. J. Clench advises me that the generic name

Limacina retroversa is a boreal form occurring from latitude 50° to northern Norway off the European coast and from latitude 34° to the southern part of Davis Strait in the western Atlantic. Bigelow considered it one of the most characteristic of the permanent pelagic inhabitants of the Gulf of Maine " where its numbers depend on local reproduction and not on immigration from elsewhere." He also emphasizes the irregularity of its occurrence, an opinion with which I can agree since my observations are at some variance with his. The seasonal variation in the distribution of *Limacina* shown in Fig. 44 of Bigelow's monograph led me to suspect that its occurrence might be closely correlated with the residual drift of the superficial water, since the captures in December and January extend along the northern and western shores of the Gulf, those from February to April occur over the western and southern sectors, while records for May extend from this zone northeasterly toward the Bay of Fundy.

During the years 1933–1934 a systematic survey was made of the Gulf of Maine with the object of obtaining a more precise seasonal picture of its hydrography and biology than was available from the observations of Bigelow. Thirteen cruises were made by the research vessel " Atlantis " in the course of fifteen months, with the result that 684 hydrographic stations in the Gulf of Maine and its adjacent waters were occupied. Whenever weather permitted, a standard vertical haul was made at each station using a Heligoland larva net similar to that described by Künne (1933). The opening of the net was 143 cm. in diameter and it was made of No. 0 silk having 38 meshes to the inch. The net was drawn from a point near the bottom to the surface. The catch of each net haul was preserved and from it the *Limacina* have been separated, counted and measured.

Seasonal Distribution and Abundance

The seasonal distribution and abundance of *Limacina* throughout the year, as shown by the number of specimens caught in each haul, is presented in Figs. 1 and 2. *Limacina* was scarce in the Gulf of Maine

---

Spiratella has claims of priority arising from Blainville's description (*Dict. Sci. Nat.*, ix, 407, 1817). No attempt has been made to distinguish *L. retroversa* from *L. balea* Möller since the distinctness of these species is in doubt (Bigelow, 1926, p. 116).

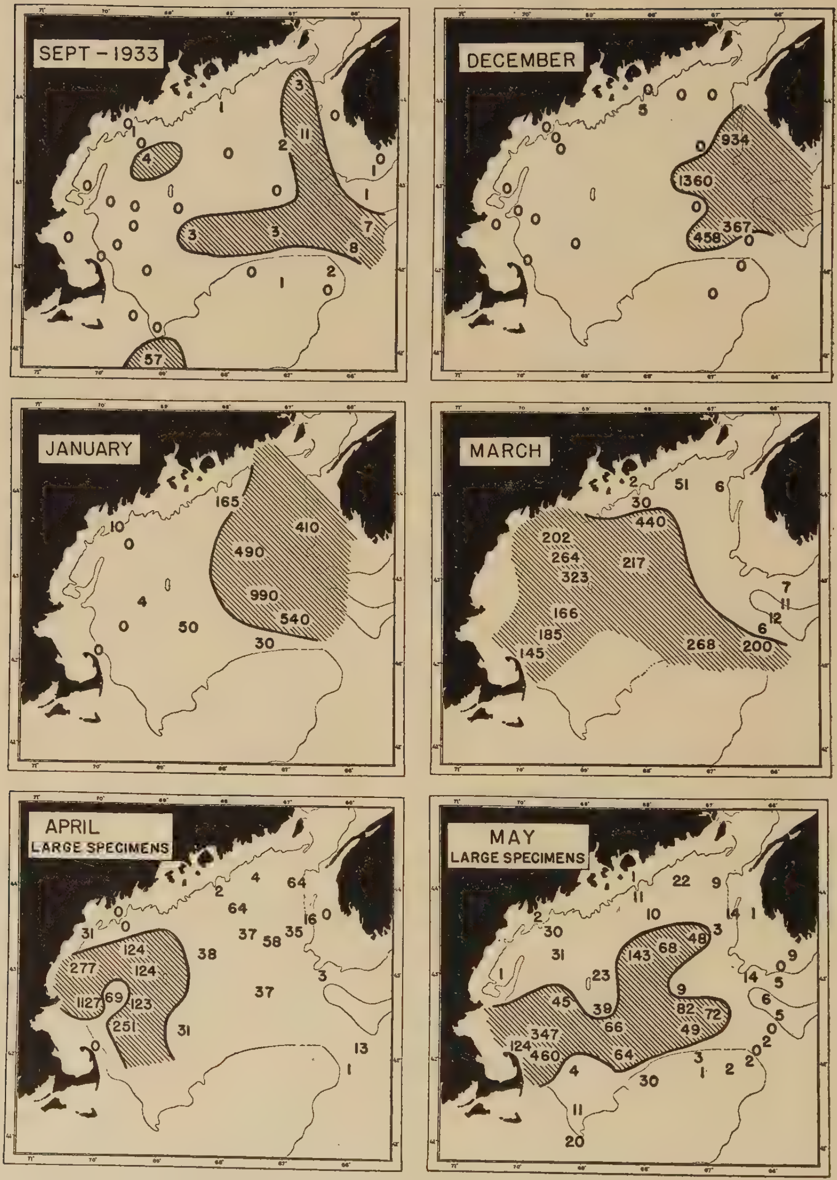

SEPT – 1933
DECEMBER
JANUARY
MARCH
APRIL
LARGE SPECIMENS
MAY
LARGE SPECIMENS

Fig. 1. Charts showing the distribution of *Limacina retroversa* in the Gulf of Maine in September and December, 1933, and in January, March, April and May, 1934. The numbers indicate the positions at which vertical hauls were made and the numbers caught per haul. The shaded area includes all hauls in which the catch was greater than the mean catch for the entire cruise. The numbers entered for April and May include only individuals attributable to population *A* as defined in text.

in the fall of 1933. A dense population of these organisms appeared in the eastern side of the Gulf in December, 1933 and spread westward during the winter. By April these pteropods are concentrated in the western side of the Gulf; the region to the eastward in which they first appeared being occupied by waters scantily populated. As the season advanced the size of the catch at each haul dwindled and the distribution became more general.

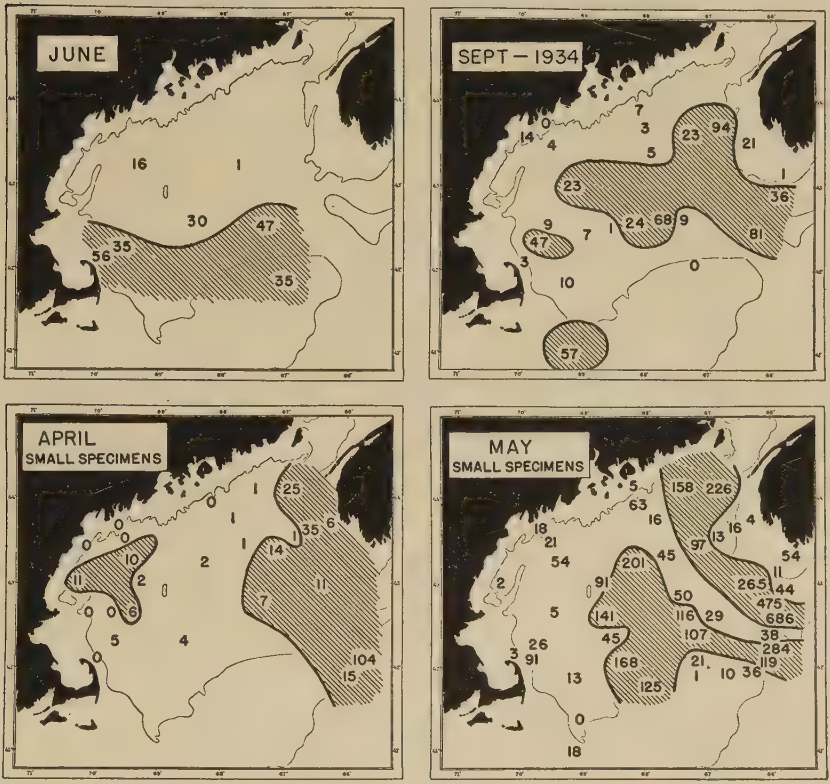

JUNE
16
1
0
30
47
35
56
35
SEPT — 1934
7
0
14
4
3
5
23
94
21
1
36
23
9
24
68
9
81
47
7
3
0
10
57
APRIL
SMALL SPECIMENS
25
1
0
1
35
6
0
0
14
1
10
2
11
2
0
11
7
0
0
6
5
4
0
104
15
MAY
SMALL SPECIMENS
5
63
158
226
18
16
16
4
21
97
13
54
201
45
54
2
91
0
50
11
265
44
5
141
116
29
475
686
107
38
284
45
3
26
91
168
21
1
119
10
36
13
125
0
18

FIG. 2. Charts showing the distribution of *Limacina retroversa* of all sizes in the Gulf of Maine in June and September, 1934, and of small individuals attributable to population *B* in April and May, 1934.

These observations suggest that a huge swarm of *Limacina* drifted into the Gulf from the east in December and were carried westward by the cyclonic drift of water about the Gulf. The acceptance of this interpretation requires evidence on two points: (1) that the population moved not only in the direction but at a rate corresponding to the mass movement of the water, and (2) that a reasonable continuity exists between the population observed in December in the eastern region and that found in April and May in the western part of the Gulf.

The Circulation of the Gulf

The character of the circulation of the Gulf is adequately described by Bigelow (1927), who with Huntsman showed that the dominant circulation is a great anti-clockwise eddy around the basin of the Gulf, varying in velocity and in detail from season to season and complicated by subsidiary eddies. The great eddy receives accessions of water from the east, particularly in winter and early spring; the area of inflow being over the Northern Channel and the adjoining banks. Compensatory losses are occasioned by outflow across the Southern Channel and around the eastern end of Georges Bank. The circulation at the greater depths has a somewhat modified character owing to the confining features of the bottom contour. A report on the dynamics of the circulation of the Gulf, based on observations made during the cruises of 1933–34, is being prepared by Dr. E. E. Watson.

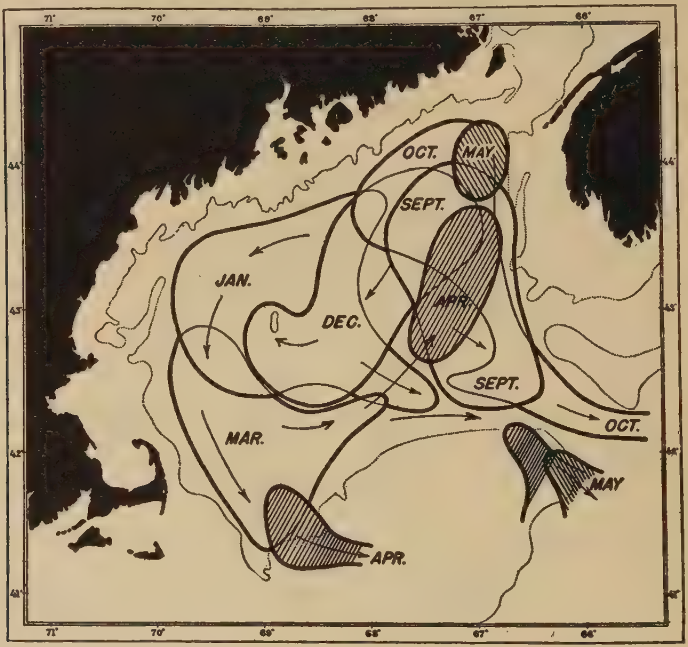


FIG. 3. Positions occupied by an area in which the salinity of the water at 50 meters depth exceeded $33^0/_{00}$ during the period from September, 1933, to May, 1934. Arrows indicate the apparent direction of drift at each period.

While our vertical hauls have given no indication of the depths at which *Limacina* occurs, it seems probable that it will be carried with the more superficial circulation of the Gulf. Bigelow (1926, p. 121) states that "the most prolific depth zone may be stated as from 20 to 25 meters down to about 80, which corroborates Paulsen's (1910) generalization that *Limacina* lives chiefly shoaler than 50 meters in north European waters, though it has occasionally been taken much deeper." That the sub-surface waters actually drift with velocity as well as direction comparable to that characterizing the *Limacina* population is indicated by a study of the distribution of salinity in the upper water levels throughout the period of the survey. An extensive area characterized

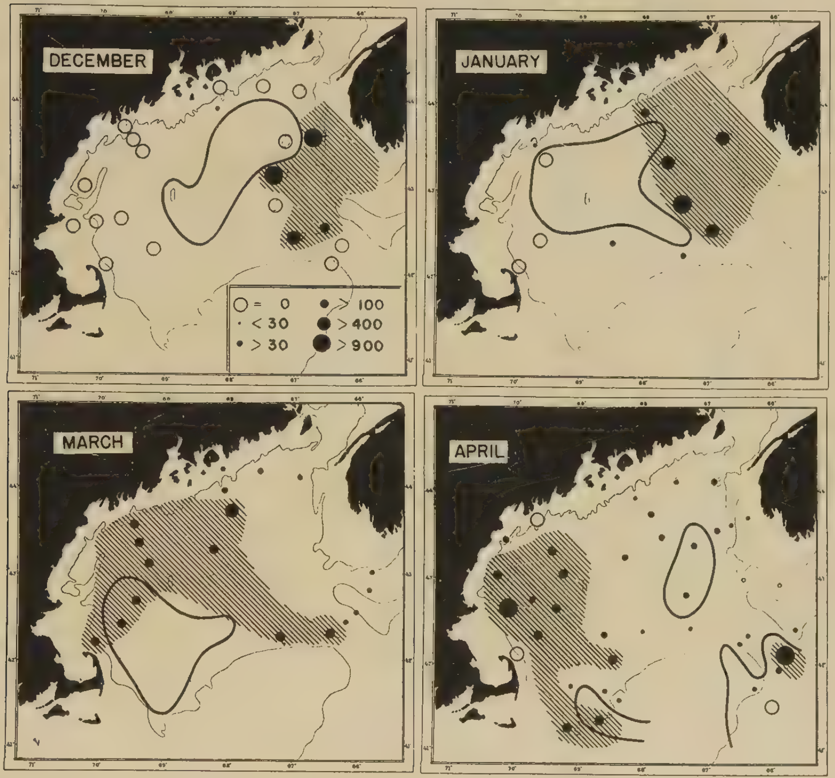


FIG. 4. Charts showing the relative positions of the area of high salinity at 50 meters depth and the distribution of *Limacina* between December, 1933 and April, 1934. The closed contours enclose the area in which $S > 33^{0}/_{00}$. The hatched areas include catches greater than 100 specimens per haul. The size of each catch is roughly proportional to the area of the black circles. Open circles represent hauls in which no *Limacina* were caught.

by salinities higher than the surroundings occurred in the eastern part of the Gulf in September, 1933. Bigelow (1927, pp. 767, 768) noted a similar occurrence in 1913, 1914 and 1915. The position of this area gradually shifted during the following months, until March when it occurred in the southwestern part of the Gulf. Subsequently it could be traced with less certain continuity as it divided, apparently drifting in part out to sea, and in part in a northeasterly direction. The "saline pool" is most clearly limited in the data for salinities at 50 meters, at which depths it is enclosed by the $33^0/_{00}$ isohaline. The successive positions of this isohaline are illustrated in Fig. 3, and correspond closely to the superficial circulation as deduced and illustrated by Bigelow (1927). The velocity of drift of this area, characterized by relatively high salinity, corresponds closely to that of the *Limacina* population which apparently followed close in its rear (Fig. 4). The observations on the distribution of *Limacina* and the occurrence of water of $S > 33^0/_{00}$ at 50 meters depth agree in indicating a drift during the winter period of the sub-surface waters through a distance of 150 miles in four months or at a rate of about 1.25 miles per day.

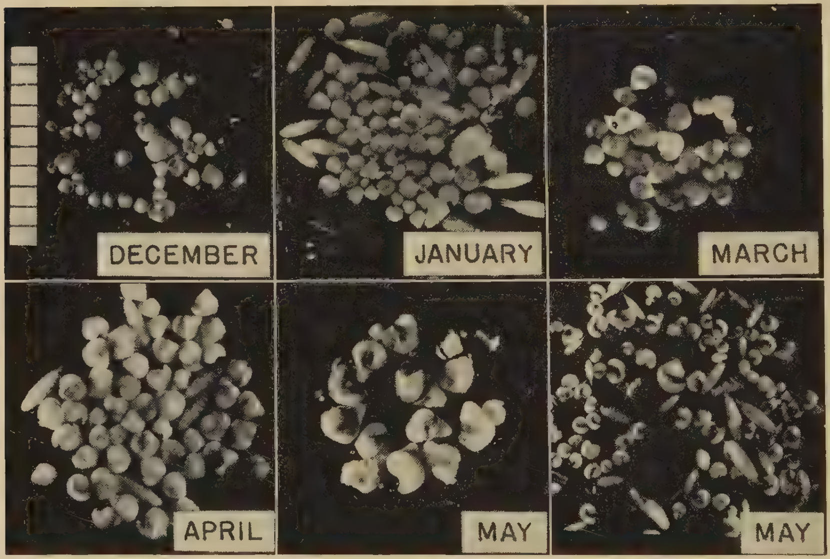


FIG. 5. Photographs of representative catches of *Limacina retroversa* taken between December, 1933 and May, 1934 showing growth. The large specimens taken in May are from the western basin and represent the size attained by population *A*. The small May specimens were taken in the eastern part of the Gulf and are attributed to population *B*. Scale, 1 centimeter divided into tenths.

The Distribution of Size at Different Seasons

The identity of the population sampled at different periods is indicated by an examination of the distribution of size among the specimens taken. These appeared to grow larger as the winter advanced (see Fig. 5). In April and May, however, large numbers of small specimens appeared in certain catches. Since the animals taken at different times and places can only be attributed to the same population if they display a reasonable relation in size, the distribution of size among the individuals of each catch was determined. The largest diameter of the specimens was measured as they lay in random positions in a watchglass. Care was taken to avoid measurements along diameters exaggerated by the spreading of the foot as it protruded from the shell. The measurements were separated into 9 size groups of 0.3 mm. span. The number in each group was expressed as a percentage of the total catch falling within each group.

Figure 6 shows the distribution of size among all the specimens taken during each cruise. In December size distribution is homogeneous; the modal class size is 0.6–0.9 mm. with a uniform distribution of smaller and larger sizes ranging between 0.3 and 1.2 mm. In January the modal class size is the same, but the larger classes have grown at the expense of the smaller. By March a general increase in size is apparent, the modal class being 1.2–1.5 mm. and almost all specimens falling between 0.6 and 1.8 mm. The general shape of the polygon is unchanged as should be the case if the increase in size is due to uniform growth. In April the frequency polygon becomes skewed. Though the modal size is the same as in March, the larger classes have increased in number, relative to the mode, as demanded by growth. The skew is due to the appearance of significant numbers of very small (less than 0.6 mm.) individuals which were not present in the March population. In May these small specimens increase greatly in numbers with the result that the frequency polygon is bimodal. The principal modal size is now 0.3–0.6 mm., being determined by the small individuals. A secondary mode occurs between 1.5 and 1.8 mm., apparently representing the mode of the original population which determined the mode during the previous periods.

The observations made between December and May may be readily interpreted as follows. A homogeneous population of small individuals entered the Gulf from the east in December and grew continuously in size. In April a new population of small individuals appeared and by May these had increased in numbers so as to dominate the size distribution. These may represent a generation of offspring from the original

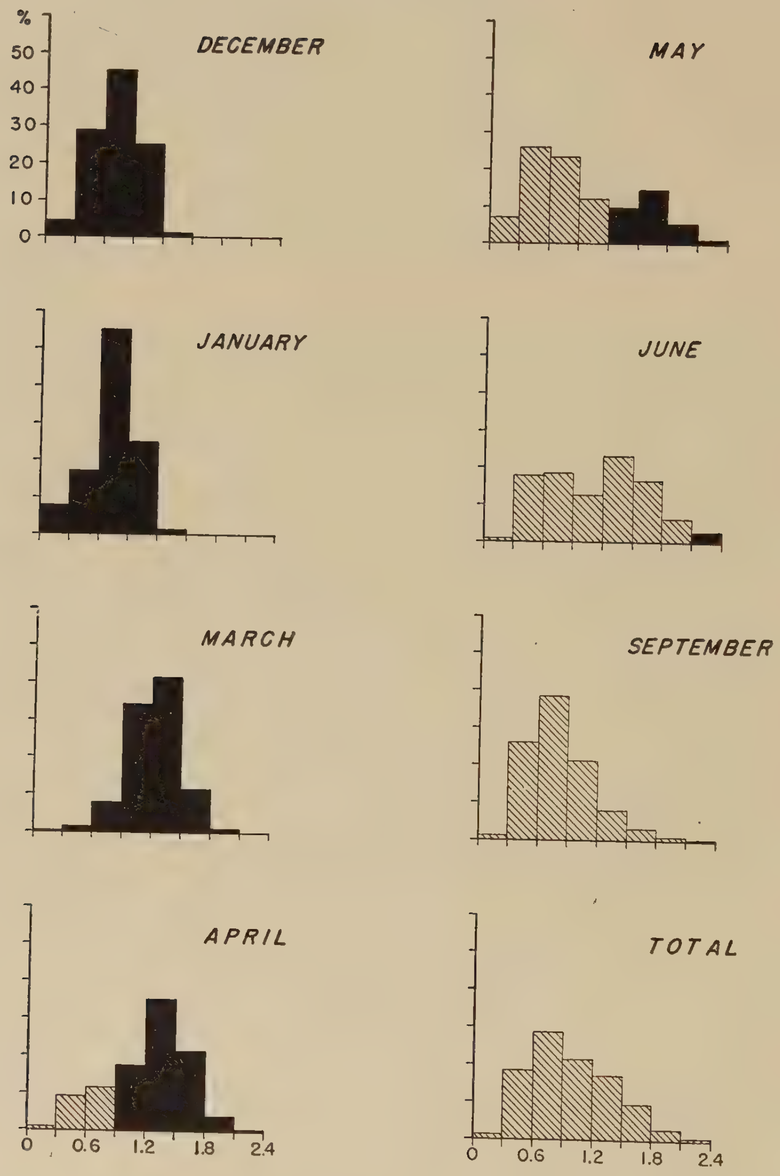


FIG. 6. Frequency polygons showing the distribution of size in the total catch of *Limacina* obtained during each cruise. The lower right-hand polygon represents the combined distribution for the entire series of cruises, corrected for variation in fishing effort. Ordinates, percentage of entire catch falling in each size group. Abscissae, size groups divided in intervals of 0.3 mm. diameter. Black areas are attributed to population *A*.

population, or an invasion of a new group from outside the Gulf, or both. For convenience we will call the original population which appeared in December the *A* population; the new population which appeared in April the *B* population.

The observations made subsequent to May are more difficult to interpret. The frequency polygon for June is again bimodal. The principal size class is now 1.2–1.5 mm. This is smaller than the mode of the *A* population for the preceding month and may be tentatively assigned to the *B* population, which may be expected to grow rapidly with the warming of the water. The largest size class, 2.1–2.4 mm., is relatively more abundant than at any previous time and probably contains the last survivors of the *A* population. A secondary mode occurs between 0.3 and 0.9 mm., which may represent a further production or a new invasion of young individuals, a hypothetical *C* population. The small specimens taken in June were caught a few miles off the coast of Cape Cod. Because of the remoteness of this position from the inflow into the Gulf, they are in all likelihood the offspring of the *A* population, which was richly represented in this region during the preceding cruise, rather than to a new invasion. Only five hauls were made during the June cruise and these all in the southwestern half of the Gulf. The data for this period are not as representative as those obtained at other times.

The scanty and scattered catches made in September, 1934 yield a simple frequency polygon with maximal size class at 0.6–0.9 mm. The distribution of size is generalized and resembles that of the combined measurements of the total collections throughout the year. Apparently during the summer growth is rapid and reproduction and recruitment of the population from without the Gulf is more or less continuous so that separate broods or populations can no longer be distinguished. Dr. Sidney Hsiao has studied the reproductive history of the collections and finds that *Limacina* produce eggs in small numbers continuously after reaching a size of 1.0 mm. It may be inferred that the offspring of one generation will vary greatly in age and after several generations their descendants may be represented by a complete assortment of sizes in which separate broods will be indistinguishable.

The Distribution of Size in the Population of Different Sectors of the Gulf

Let us return to the examination of the history of populations *A* and *B* with a view to determining whether they are actually homogeneous populations and to distinguishing whether population *B* arises through reproduction within the Gulf, or invasion from outside.

The size distribution of representative catches made in different parts of the Gulf at each period has been examined. For this purpose the Gulf has been divided into seven sectors as indicated in Fig. 7. These sectors are arranged in the order in which the non-tidal drift of water may be expected to carry a pelagic population in the circuit of the Gulf. It should be noted, however, that much water will be carried from the Yarmouth and Mt. Desert sectors directly to the Georges sector without penetrating the western sectors of the Gulf, as Fig. 3 indicates. Representative catches made at each period in each of these sectors have been selected and their size frequency polygons are given in Fig. 8.

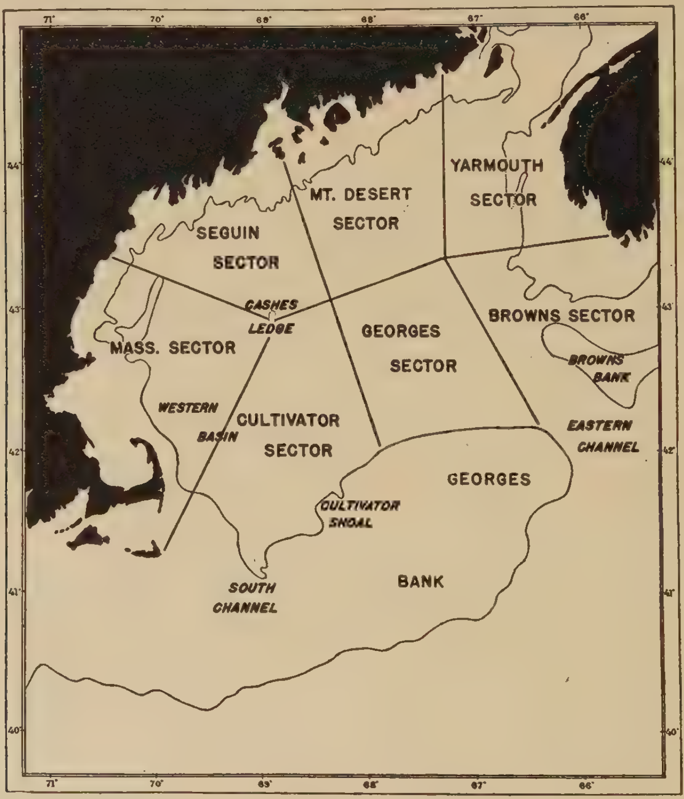

71°
70°
69°
68°
67°
66°
44°
43°
42°
41°
40°
YARMOUTH SECTOR
MT. DESERT SECTOR
SEGUIN SECTOR
CASHES LEDGE
GEORGES SECTOR
BROWNS SECTOR
MASS. SECTOR
BROWNS BANK
WESTERN BASIN
CULTIVATOR SECTOR
EASTERN CHANNEL
GEORGES
CULTIVATOR SHOAL
BANK
SOUTH CHANNEL

Fig. 7. Chart of Gulf of Maine showing principal place names and the sectors into which the area is divided for analysis of population distribution. Contour encloses depths less than 100 meters.

Figure 8 shows that from December through March the size distribution in different parts of the Gulf is homogeneous and that the increase in size noticeable in March is of general occurrence. The extension of the population westward during the winter is apparent. The

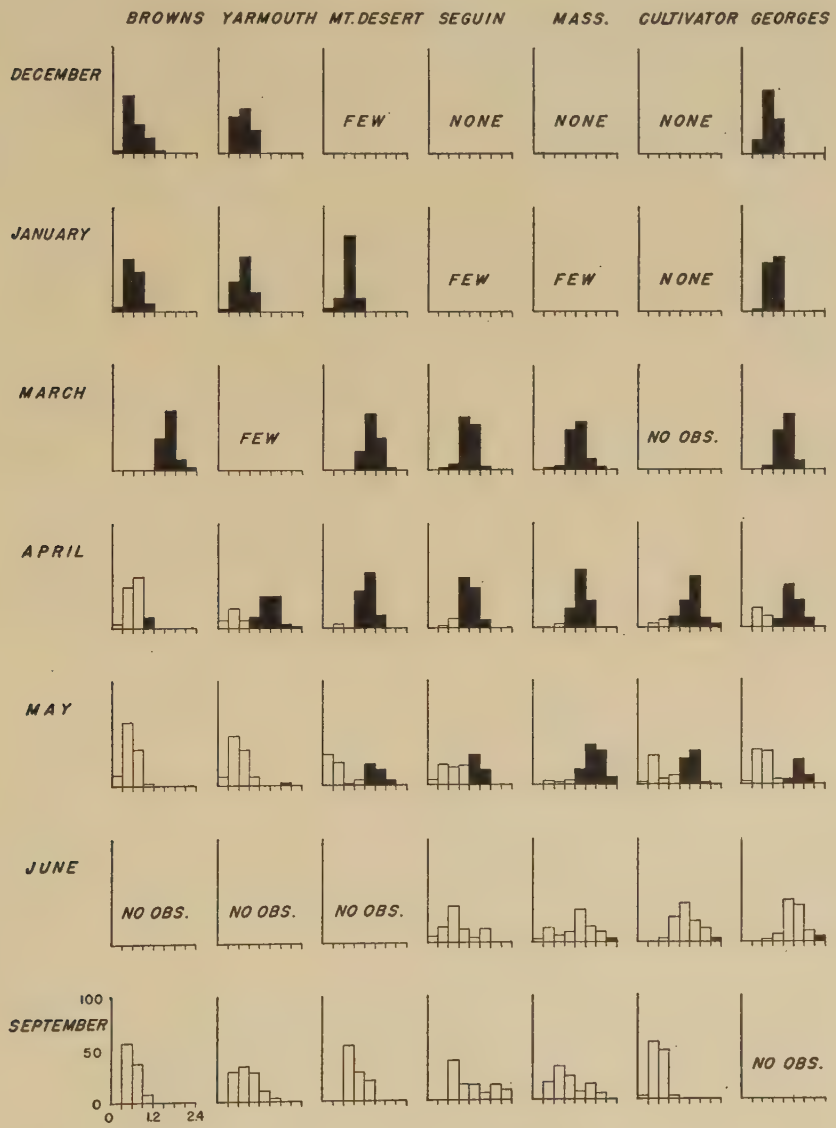


FIG. 8. Frequency polygons showing the distribution of size in representative catches of *Limacina* from each sector of the Gulf of Maine during each cruise. No hauls were made in the sectors marked *No Obs.* Ordinates, percentage of entire catch falling in each size group. Abscissa, size groups divided in intervals of 0.3 mm. diameter. Black areas are attributed to population *A*.

continuous occurrence of *Limacina* in the Georges sector is in accordance with the characteristics of the current system as noted above. In April the homogeneous *A* population appears in all the northern and western sectors of the Gulf. Small individuals representing the *B* population appear now in the eastern sectors, Browns, Yarmouth and Georges. In the outermost sector to the east, Browns, the *B* population is unaccompanied by any specimens of larger size, characteristic of the *A* population at this time.

In May the small individuals of the *B* population are much more widespread, appearing abundantly in all sectors except the most westerly, Massachusetts sector. Only small individuals occur in the stations of the Browns and Yarmouth sector. The populations of the Mt. Desert, Cultivator and Georges sectors have a mixed, bimodal character. The duplex character of the population in April or May is brought out in Figs. 1 and 2, in which the numerical distribution of individuals of different sizes is shown. Small specimens appear in numbers only in the water in the offing of the Eastern Channel in April and occur in small numbers along the course of the inflow through the Eastern Channel. In May they are generally distributed in the eastern part of the Gulf which is most accessible to inflowing water and are scarce in the western region in which the larger specimens of the *A* population are dominant.

These observations justify the belief that the *A* population represents the invasion of the Gulf from the eastward by a homogeneous population which grows as it drifts westward.

Reproduction in the Gulf

The appearance of the *B* population in the eastern sectors, unaccompanied by members of the *A* population and the extension of the smaller group westward during May makes it clear that the new population of small individuals which appears in the spring is due chiefly to a second invasion of *Limacina* into the Gulf from waters offshore and to the eastward. Whether the small individuals which occur mixed with the *A* population in several sectors are the offspring of the *A* population is difficult to decide. Dr. Hsiao finds the *A* population to contain sexually active individuals during the spring, so that offspring from this population are to be expected. On the other hand, the relative scarcity in May of the *B* population in the Massachusetts sector where the *A* population was then most concentrated, argues against the possibility that the *B* population in neighboring sectors is in any important degree the offspring of the *A* population. It is noteworthy that when the *A* population first appeared in December it was dominated by individuals of small size and no individuals of large size occurred among them. This was also true in many hauls in which the *B* population appeared in April and May. This indicates that the parental generation does not survive after breeding long enough to be caught along with offspring which have grown to diameters of 0.3 mm. or greater. This consideration also supports the view that the hauls in which large and small individuals occur together represent the mingling of populations of different origin rather than the simultaneous presence of a parental and filial generation.

Growth

Since the foregoing analysis of the collections appears to warrant the conclusion that the *A* and *B* populations are homogeneous entities, we may examine the growth rate of *Limacina* by comparing the size of the modal classes of these populations at different times throughout the year. In Fig. 9 the size of the modal class is plotted against the time the collection was made. Roughly speaking, the diameter of the *A* population doubles in about five months during the winter. At this time the temperature of the water column as a whole is below 7° C. The *B* population observed in May and June grows very much more rapidly as might be expected from the higher temperature of the surface waters at that time.

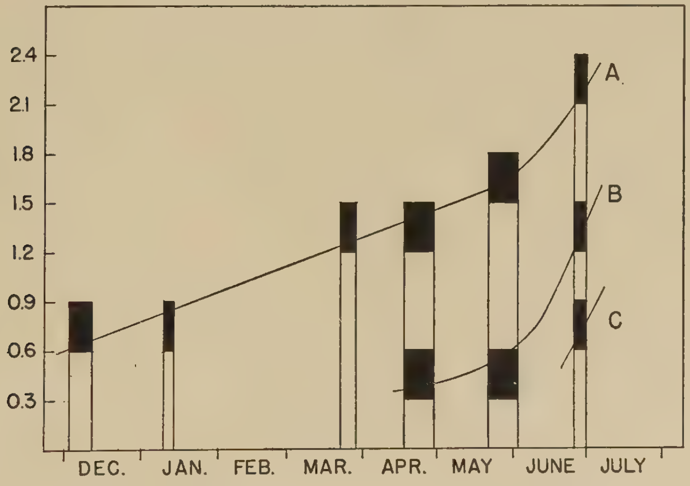


Fig. 9. Diagram indicating the increase in diameter of the modal class of *Limacina* of populations *A, B* and *C* during the winter of 1933–34. Ordinates, size groups divided in intervals of 0.3 mm. diameter. Abscissae, time during which collections were made. The black areas represent the modal class size of each population.

Numerical Abundance and Mortality

The *A* population is sufficiently established as a distinct and homogeneous entity and was under observation for a sufficiently long period to warrant some statistical examination of its numerical abundance. It must be realized that the number of hauls made in each cruise is insufficient and their distribution too irregular to allow great confidence in the outcome of the analysis of a matter of such complexity, but data of this sort are so rare and so difficult to obtain that one is warranted in the attempt to get the utmost out of it.

TABLE I

Statistics of the size of catches of Limacina retroversa made during the cruises of 1933–1934.

Cruises	No. of Hauls	Total Catch	Mean Catch per Haul	Per Cent of Hauls with Limacina Present	Per Cent of Hauls with Catch Greater than Mean
Sept. 2–14, '33	34	104	3	44	21
Dec. 2–11, '33	22	3120	142	23	18
Jan. 8–13, '34	12	2685	224	66	33
Mar. 21, 29, '34	18	2535	141	100	55
April 17–23, '34*—Small	24	141	6	71	33
Large	24	2575	107	84	24
Total	24	2716	113	100	23
May 21–June 3, '34—Small	44	4068	92	98	25
Large	44	1849	42	91	25
Total	44	5917	134	100	23
June 25–July 1, '34	7	220	31	100	57
Sept. 17–27, '34	26	507	20	92	20

* Two hauls made in the Eastern Channel on May 6, 1934 are included in the data for the April cruise.

We may consider that all the individuals taken in December, January and March belong to the *A* population. In order to eliminate as far as possible the *B* population individuals smaller than 0.9 mm. are eliminated from the data for April and smaller than 1.2 mm. from that for May. The *A* population cannot be identified with assurance in the June collections.

Increase in numbers can be due only to the invasion of the Gulf by new immigrants from offshore since the elimination of the *B* population precludes reproduction as a means of increase. Decreases in numbers may be due to water movements, carrying a part of the population out of the area under observation, or to mortality. Since the population first appears densely distributed at one side of the Gulf, some redistribution of density between different points of observation is to be expected as the result of lateral mixing of the water. This may be expected to result in an increasing uniformity of distribution.

Table I contains some statistics concerning the size of the catches made during the several cruises. An indication of the numerical abundance of *Limacina* in the Gulf as a whole at each period is given by the numbers in column 4 showing the average number taken per haul. Between December and January the numbers increase, after January there is a progressive decline in abundance. An examination of the distribution of *Limacina* from month to month (Fig. 1) warrants the conclusion that the invasion of the *A* population into the Gulf continues through December and January since large catches are made at these times in the region of inflow. The percentage of stations at which *Limacina* was taken (column 5) increases three-fold during this interval. The invasion appears to terminate in January, since following that period no considerable numbers of individuals referable to the *A* population were taken in the region of inflow into the Gulf. Invasion may consequently be excluded as a significant factor affecting the numbers of the population after January.

The numbers of the population decline steadily from January through May, the mean catch of large individuals referable to population *A* decreasing to less than 20 per cent of the original in four months. Significant losses are attributable to the drift of water out of the Gulf. The continuous occurrence of catches containing *Limacina* in the Georges sector, which lies in the path of outflow through the Eastern Channel, and the concentration of the *A* population in the western and southern quarters of the Gulf in April and May, where it is subject to drift outward by way of the South Channel, favor such losses.

It is probable that large losses in numbers also occur as the result of mortality. Measurements of the total volume of zoöplankton caught throughout the Gulf indicate a general mortality of about 60 per cent during the winter period.

The data in Table I indicate that the percentage of stations at which *Limacina* occurred is not less in April and May than in January. If the circulation into and out of the Gulf were rapid enough to account for the greater part of the loss in numbers, a greater decrease in the area of distribution would be expected. It may be argued that since the area of distribution does not decrease while the numbers caught per station decline five-fold, the decline is due to the death of a large part of the population. This argument, however, must be accepted with great reserve, since the lateral mixing of water may cause small numbers of animals to be carried into regions in which they did not previously occur, and will tend to enlarge the area of occurrence.

Another approach to the question of mortality may be made through an examination of the distribution of size in the catches as a whole throughout the year. In Fig. 6 the size distribution of the *total* catch is represented. This frequency polygon was prepared by averaging the percentages of the population represented by each size group during each period of collection, a procedure which corrects for the variation in "fishing effort" during different cruises, but does not correct for the irregularity of spacing of the cruises in time. The figure shows that the size most frequently caught is 0.6–0.9 mm. Smaller sizes are less frequent in part because both the *A* and *B* populations are carried into the Gulf half-grown, in part because they are more readily overlooked in sorting the catch and in the case of the smallest class, because many may pass through the mesh of the net. The larger size classes diminish progressively in their relative abundance, as would be expected if the population is subject to continuous mortality. The mode of the *A* population is 0.6–0.9 mm. in January, 1.5–1.8 mm. in May. Specimens of the latter size occur about one-third as abundantly as the former in the catches as a whole. This suggests a mortality of about 66 per cent in the time taken to grow from the former to the latter size, during four winter months. Such statistics, however, are not very convincing since the smaller classes are recruited by invasion and the chance of loss by drifting out of the Gulf increases with time, as does the size of the individuals of the population.

Lateral Mixing

The horizontal mixing of water masses, which has recently attracted the attention of hydrographers, may be expected to have consequences of importance in determining the distribution of organisms. If attention is limited to the consequences of steady residual currents, one can only conclude that the pelagic inhabitants of a region such as the Gulf of Maine which is the seat of a cyclonic eddy must be constantly washed away by the flow of water through it. The rise and decline of the *Limacina* population which we have observed supports this conclusion. The existence of lateral mixing, if of considerable extent, should tend to diminish the tendency of residual currents to transport all of the pelagic population out of such a region. By the transport of a part of the population backstream, or around and across the vortex of an eddy, an opportunity would be afforded for the endemic occurrence of the population in spite of the continuous drainage occasioned by the residual currents.

The effect of lateral mixing must tend continuously to make the distribution of the population more homogeneous. After the introduction of a limited water mass containing a rich population into a large unpopulated region, if lateral mixing alone were in operation one would expect the limits of the populated waters to become less distinct and the distribution to become more general. If samples were taken at random at any time during the mixing process, at first a limited number of samples would contain numbers far in excess of the mean value for the collections as a whole, and the remainder would contain small numbers or none at all. As mixing proceeds, the poorly populated waters would become enriched at the expense of the densely populated regions. In both regions the density of population would change in the direction of the mean population for the entire region and eventually the entire distribution would assume a random character in which the modal population density would correspond with the mean. At this point half the samples would contain more than the mean number, and an equal number less than this value. Subsequent mixing would tend only to diminish the variation of the numbers secured in the different samples.

The catches of *Limacina* have been examined for such evidences of lateral mixing. Examination of the distribution of the population shown in Fig. 1 indicates that the populated region was sharply delimited in December—no *Limacina* occurring in regions immediately in advance of the populated waters. In January moderate catches were made in regions well in advance of the main population, suggesting a gradual disintegration of the boundary zone by lateral mixing. In March the area of intense population covers more than half the Gulf and at the same time the numbers present at each station have diminished and become more uniform as required if lateral mixing is in effect. The same tendencies continue in April and May and are particularly evident when the distribution of small specimens (population *B*) is compared. While previous to March less than half the hauls have contained more than the mean catch for the Gulf as a whole, by March at least half the hauls are of this size—as required by random distribution. One feature of the distribution of large specimens in April and May is of particular interest. In the east central part of the Gulf, on the line between Cashes Ledge and Yarmouth, Nova Scotia, the catches of large specimens are on the whole greater in May than in April in spite of the fact that some mortality is doubtless occurring during this period and the movement is contrary to the expected drift of the water.

As a further test to see if the distribution of population is becoming more homogeneous, the catches have been grouped into classes according to the number taken per haul and the number of catches in each class has been expressed as a percentage of the total number of catches made during the cruise in question. The result is presented in Fig. 10. The left-hand diagram shows the result when the size of the catch is noted numerically (and assigned to classes which for convenience increase in geometrical progression). The right-hand diagram represents the same data arranged in size classes which increase as multiples, or decrease as fractions, of the mean population of the region as a whole at the period of collection. The latter procedure eliminates the effect of losses

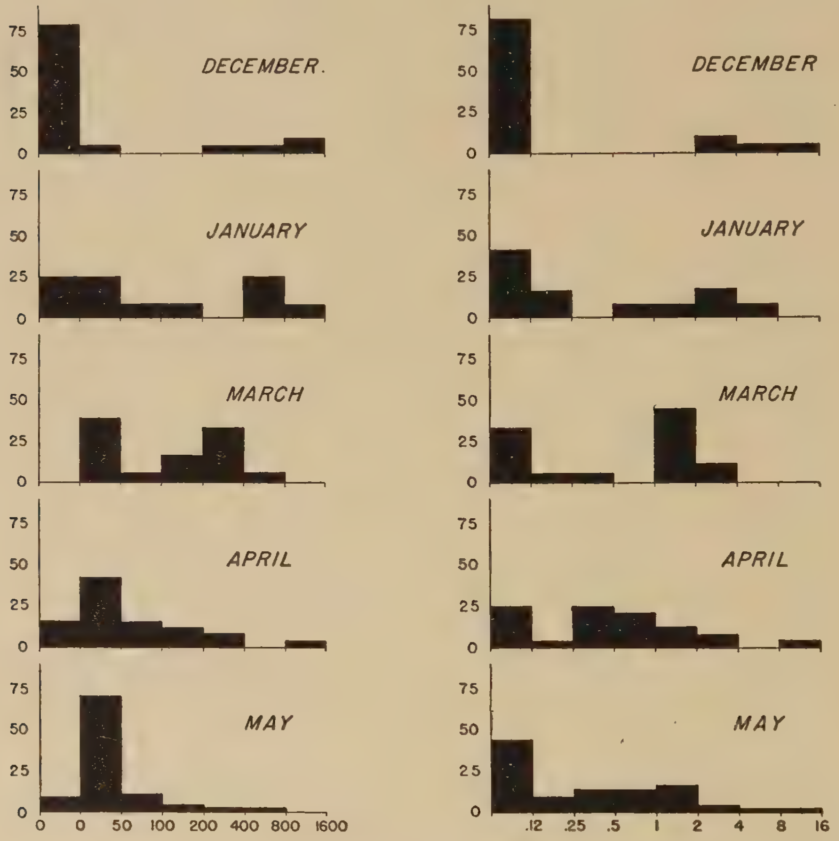


FIG. 10. Frequency polygons showing the distribution of catches of different numerical abundance among the total number of hauls made during each cruise. Ordinates, percentage of entire number of hauls yielding catches of each size. Abscissae, left-hand diagrams, size groups divided in intervals according to number caught in each haul; right-hand diagram, size groups expressed as multiples or fractions of the mean catch per haul during each period.

through mortality. Both diagrams indicate the complete heterogeneity of the samples in December and January and the progressive approach of both the smaller and larger catches toward the mean value which reaches its culmination in April and May.

Actually the situation observed is complicated by the drift of the population across the region and by the invasion of the eastern part of the Gulf by water poor in *Limacina* of population *A* in March and April. This inflow tends to decrease the homogenity of distribution and accounts for the increase in the proportion of catches in April and May which contained few or no *Limacina*. It also explains why the percentage of hauls in which the catch was greater than the mean diminished in the months subsequent to March. These tendencies during April and May at least make it clear that lateral mixing is not sufficiently great to obliterate the effect of the residual current in depleting the *Limacina* population of the eastern portion of the Gulf.

Because of the impossibility of separating the effects of mortality and of losses and gains through the residual movement of the water into and out of the Gulf from the apparent effects of lateral mixing, any attempt to evaluate the extent of the latter has been abandoned. Because of the great influence which such mixing would have in enabling a population to maintain itself in a region from which the residual current would constantly tend to remove it, it seems desirable, however, to emphasize the possibility of such mixing and to indicate the way in which it appears to manifest itself.

Discussion

The evidence seems definite that the population of *Limacina* which occurred in the Gulf of Maine in 1933–34 was not endemic, as Bigelow thought, but owed its origin to two separate invasions of young individuals from offshore. Unlike the less successful immigrants of arctic or tropical origin, *Limacina retroversa* thrives well enough to grow to sexual maturity and perhaps to reproduce within the Gulf and to be carried in considerable numbers to all its parts. For this reason Bigelow obtained evidence which led him to conclude the species was endemic. By following the history of these populations closely, however, it is shown that neither invasion was able to maintain its numbers in the Gulf—either because reproduction was not successful or was inadequate to balance the depletion due to mortality and the drift out of the Gulf.

The two invasions consisted of dense swarms of small individuals of very uniform size, sharply separated by a period when practically no *Limacina* occurred in the region of inflow into the Gulf. The discontinuous character of these invasions no doubt accounts for the irregularity in occurrence of *Limacina* in the Gulf noted by Bigelow. Why the invasion occurs in such definite periodic swarms can be answered only by studies carried out in the waters to the eastward from which these invasions undoubtedly come.

It is an interesting question why the invading swarms are composed of individuals of such uniform size. In describing the population found in the Gulf in September, 1934, it was pointed out that animals of all sizes were mixed together and that successive broods can no longer be distinguished. Dr. Hsiao's studies indicate that the mature *Limacina* continue to produce eggs during a considerable period of growth. Yet we found evidence to suggest that the parental generation does not survive after breeding long enough to be caught along with its offspring at the time when these enter the Gulf. Dr. Hsiao has measured numerous catches of *Limacina* taken over the continental shelf between Cape Cod and Cape Hatteras. Usually these catches are composed of individuals of uniform size, just as were those which invaded the Gulf. This riddle also can be answered only by closely timed observations in the offshore areas of production.

The most conspicuous result of this study is the demonstration of the degree to which the occurrence of *Limacina* in the Gulf of Maine depends upon the circulation of its waters. Damas in 1905 raised the question: How does the plankton of a given region maintain its character in the face of the continual circulation of the currents and how does a given species persist so as to possess a special geographic distribution? He concluded that there must exist a special zone or center of production in which adults abound and reproduce successfully and that to this region circulatory currents serve to bring back periodically a proportion of the individuals which become entrained and dispersed by the continual movements of the water. The circulatory system of the Norwegian Sea subsequently described by Helland-Hansen and Nansen (1909) appeared to supply just such a mechanism as was required to account for Damas' observation of the production centers of copepods in that region. Sømme (1933, 1934) has shown how such centers of production are established for *Calanus finmarchicus* and *hyperboreus* in the deep waters of the Norwegian fjords in winter, and has elucidated the mechanism which results in the release of the organisms from these regions at the time of reproduction. The observations on *Limacina* have not revealed the presence of a center of production in the Gulf of Maine. They point to the existence of such regions offshore to the eastward and are of interest rather in telling something of the fate of these animals, entrained in the movement of water, which are carried away never to return, yet for a while to occupy an important rôle in the ecology of other regions. Behind the geographical distribution of each species of plankton there must be a complex balance of biological and physical factors. Of the latter, flow of water appears to be paramount; its consequences too frequently neglected.

Summary

A population of small specimens of the pteropod, *Limacina retroversa,* appeared in the eastern part of the Gulf of Maine in December, 1933. From collections made during the following 9 months information was obtained showing that the population was a homogeneous one, that its members grew to maximum size in 5 months, declining in numbers as they did so.

A second population of small individuals appeared in the Gulf in late spring, originating chiefly from offshore, but possibly in part being offspring of the original population. These were unsuccessful in maintaining their numbers throughout the summer.

In addition to the information on the life history of *Limacina,* the data indicate the rate of drift of the water in its circuit of the Gulf. It supplies also suggestive information on the dispersal of organisms through the lateral mixing of water. It emphasizes the dependence of pelagic organisms upon the current systems of the ocean and the difficulty involved in maintaining a permanent population in any one locality.

REFERENCES

Bigelow, H. B., 1926. Plankton of the offshore waters of the Gulf of Maine. *Bull. U. S. Bur. Fish.,* **40** (1924), Part II: 1–509.

Bigelow, H. B., 1927. Physical oceanography of the Gulf of Maine. *Bull. U. S. Bur. Fish.,* **40** (1924), Part II: 511–1027.

Damas, D., 1905. Notes biologiques sur les copepods de la Mer Norwegienne. *Publ. de Circonstance,* No. 22, Copenhagen.

Helland-Hansen, B., and F. Nansen, 1909. The Norwegian Sea. Report of the Norwegian Fishery and Marine Investigations. II. Part I.

Huntsman, A. G., 1924. Oceanography. *Handbook of the British Association for the Advancement of Science,* Toronto, pp. 274–290.

Künne, Cl., 1933. Weitere Untersuchungen zum vergleich der Fangfähigheit vershiedener modelle von vertikal Fischen den Plankton-netzen. *Rapp. et Proces-verb. des Reunions. Conseil perm. internat. pour l'explor. de la mer,* **83**: 19 pp.

Paulsen, O., 1910. Pterapoda. *Bull. Trimestriel, Conseil perm. internat. pour l'explor. de la mer,* Part I, pp. 52–59.

Sømme, I. D., 1933. A possible relation between the production of animal plankton and the current-system of the sea. *Am. Nat.,* **67**: 30.

Sømme, J. D., 1934. Animal plankton of the Norwegian coast waters and the open sea. I. Production of Calanus finmarchicus (Gunner) and Calanus hyperboreus (Kroyer) in the Lofoten area. *Report on Norwegian Fishery and Marine Investigations,* IV, No. 9, pp. 3–163.

Contribution No. 197

Reprinted from Biological Bulletin, Vol. LXXVI, No. 1, 7–25, Feb., 1939
Printed in U. S. A.

THE REPRODUCTIVE SYSTEM AND SPERMATOGENESIS OF LIMACINA (SPIRATELLA) RETROVERSA (FLEM.) [1]

SIDNEY C. T. HSIAO

(From the Biological Laboratories, Harvard University and the Woods Hole Oceanographic Institution,[2] Woods Hole, Massachusetts)

Introduction

Limacina retroversa was described as early as 1823 by Fleming under the name of "*Heterofusus retroversus,*" but very little is known about its internal structure, its method of reproduction and its life history. Writing in 1924—one hundred years later—Bigelow mentioned that "' Nothing is known of the reproduction of *Limacina retroversa* in the Gulf of Maine. . . ." The embryonic development and the reproductive system of several species of Pteropoda have been described but no exact information on the species *L. retroversa* is available. Van Beneden described the structure of the reproductive system of *L. arctica* in 1839 but, as pointed out by Meisenheimer (1905), he made the mistake of calling the ovotestis the ovary, the vesicula seminalis the testis and the accessory glands the "gland prostatique." Studies of the embryonic development of pteropods have been made by Gegenbaur (1853, 1855), Krohn (1856), Müller (1857), Fol (1874, 1875) and Knipowitsch (1891). Meisenheimer (1905) described the comparative morphology of Pteropoda and compared the genus *Limacina* with other Euthecosomata. He considered *Limacina* as a general group and made no mention of any species. Meisenheimer also appraised the earlier work and observations of Cuvier, d'Orbigny, Van Beneden, Gegenbaur, Souleyet, Pelseneer, Knower, etc. Bonnevie (1916) made further observations on the reproductive organs of *Cuvierina* and recently Zarnik (1911) determined the chromosome number of several species of pteropods. Up to the present no one has studied the entire life history of any species of Pteropoda and it has been unknown whether any pteropods, like some other mollusks, change their sex. The reproductive system of *Limacina retroversa,* in particular, has not been studied. It is the purpose of this paper to describe the reproductive system and spermatogenesis of *Limacina retroversa* as a basis for a report on the reproductive history of this species to appear in a subsequent paper.

---

[1] The name "*Limacina retroversa*" has been in use until 1930, when Sherborn pointed out that Cuvier (1817) used the vernacular name "Limacine" and he restored de Blainville's "*Spiratella*" in place of Lamarck's (1819) "*Limacina.*" Thiele (1931) also used "*Spiratella.*" However, as "*Limacina*" has the advantage of being more commonly used and better known it is retained in this paper.

[2] Contribution No. 197 from the Woods Hole Oceanographic Institution.

MATERIAL AND METHODS

The material was collected by the research vessel "Atlantis" of the Woods Hole Oceanographic Institution during a series of cruises in the Gulf of Maine between June, 1933 and September, 1934. The specimens were caught by vertical hauls made with a 1.5-meter Heligoland net drawn from a level near the bottom up to the surface and were fixed on board the ship in 2 per cent formalin in sea water.

Each specimen used for making permanent mounts was decalcified in 1 per cent acetic acid for a few minutes. In some cases the acid in the commercial formalin used in fixation had decalcified the specimens. The decalcified animal was then stained in toto for about one minute in a 0.1 per cent aqueous solution of Erhlich's methylene blue chloride to aid in orienting it in the paraffin block for sectioning. The stained specimen was dehydrated in two grades of 1–4 dioxene in a calcium tower and directly imbedded in 53°–55° C. paraffin. Each individual was cut in serial longitudinal sections five micra in thickness which were mounted in order on slides. The vital stain was removed when the sections were hydrated after the removal of paraffin with xylene. Standard methods of staining with Heidenhain's iron haematoxylin and orange G were used in the final staining process. Stained sections were cleared in xylene and mounted in Canadian balsam.

In order to reconstruct the different parts of the reproductive system sections from suitable individuals were drawn with a camera lucida. The tracings of every fifth or tenth section were made with a wax pencil on pieces of glass. Reconstruction of the reproductive system was made by superimposing the glass plates in order so as to determine the size and shape of each organ. These tracings were compared with Meisenheimer's plates and descriptions (1905) of similar sections of the reproductive apparatus of Euthecosomata. Meisenheimer's terminology of the different parts of the regenerative system was followed.

In the study of the spermatogenesis of *Limacina retroversa* the method for carmine smears was used in addition to the examination of permanent mounts stained in Heidenhain's haematoxylin. The specimens used for making carmine smears were collected in the summer of 1937 near Woods Hole. As soon as the animals were taken from water they were fixed for twenty minutes in a mixture of one part of acetic acid and three parts of absolute alcohol. Each *Limacina* was separated from other planktonic material and stored in 70 per cent alcohol. It was necessary to change the preservative several times in order to get rid of the precipitate brought down by alcohol from sea water. The gonads from several individuals were dissected out under a binocular microscope and torn up into very small pieces. They were then stained with cytological aceto-carmine for a few minutes, covered with a coverglass and heated over a small flame without boiling. The slide with the material was then pressed between blotting papers to separate the cells and to remove the excessive stain. Such preparations showed the cellular structures very clearly and were used for spermatogenesis studies.

Living animals have been kept in the laboratory for a week to ten days for observation of spawning and egg-development.

Observations

The Reproductive System

The reproductive system of *Limacina retroversa* consists of a bisexual gonad, a gonoduct, accessory glands and a penis.

The Gonads.—The bisexual gonad or ovotestis constitutes the primary sexual organ. In a mature individual it is a spiral structure situated posterior to the liver and occupies the posterior or last three or four whorls of the shell with whose cavity the smooth, non-lobated coils of the ovotestis conform (Fig. 1). In specimens preserved in formalin the gonad appears, after decalcification, granular and pinkish in contrast to the yellowish-green liver with which it is continuous. In living specimens the gonads can also be distinguished from the greenish liver through the transparent shell. In sectional view, the cortical and apical regions of the mature gonads are generally occupied by the female reproductive cells and the medullary portion by the spermatic tissues. The spermatic tissues are apparently arranged in tubules in the medulla of the ovotestis, but in well-developed males they may extend to the cortex with masses of mature spermatozoa obliterating the tubular arrangement of the reproductive cells. In large females, on the other hand, the mature ova may be found in the medullary region just before they pass into the hermaphroditic duct. The proportion of masculine and feminine reproductive cells varies with the season as well as with the size of the animal.

Three different types of gonads can be distinguished. (*A*) Sexually undifferentiated gonads all of which occur in small-sized specimens; (*B*) "pure male" gonads which belong to somewhat larger animals but never to animals greater than 1.1 mm. in diameter across the largest whorl of the shell; and (*C*) hermaphroditic gonads, or ovotestes, characteristic of all larger individuals.

A. Sexually undifferentiated gonads.—In very small specimens the gonad is sexually undifferentiated in that no definite male or female reproductive cells can be recognized. This type of gonad corresponds with the "indefinite gonads" of Coe (1931) and Orton (1926). The whole gonad is small, nearly spherical and surrounded by the liver. The pregerminative cells, all of nearly equal size, form a solid mass which is enclosed within a thin fibrous Ancel's layer consisting of elongated cells with prominent nuclei. The cellular structure of the pregerminative cells is not easy to make out, for in specimens fixed with commercial formalin and stained with haematoxylin the nuclei are diffused and the structure not clear. In this, as in the other types of gonads, the fixative used tends to make the cells indistinct from each other so that they have the appearance of a syncytium. A sectional view of a young indefinite gonad is shown in Fig. 2, *A*.

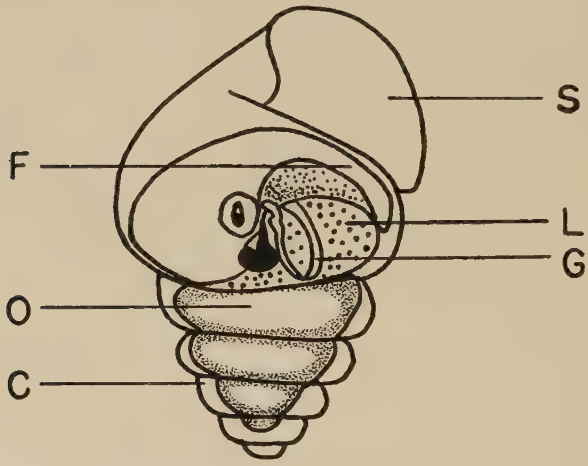


FIG. 1. Camera lucida drawing of *Limacina retroversa* (× 30), showing the gonad and the rest of the body.

C. Cavity between shell and ovotestis.
F. "Flapper" or "foot."
G. Gut.
L. Liver.
O. Ovotestis.
S. Shell opening.

B. "Pure male" gonads.—All *Limacina retroversa* larger than 0.85 mm. in diameter show sexual differentiation, for either male or female germ cells are discernible. But nearly all, if not all, of the very small sexually differentiated individuals are protandric. Half of the protandric animals do not show any ovogenesis at all. Individuals possessing this type of gonad correspond to Coe's (1933) "true males" or Orton's (1909) "pure males." In this description they will be called "pure males." The "pure male" type of gonad is confined to small-sized *Limacina retroversa.* No individuals larger than 1.1 mm. in diameter show complete maleness in their gonadal organization. In Fig. 2, *B* a gonad without any feminine reproductive cells distinguishable from the male cells is shown. In this diagram a few clusters of spermatozoa and a few groups of spermatids are seen while many of the other cells are undergoing active spermatogenesis.

C. Hermaphroditic gonads.—Besides "pure males" sexually differentiated *Limacina* have gonads with various proportions of masculine and feminine types of tissue and show different signs of sexual activity. For convenience of description and comparison, these larger specimens, possessing ovotestes, can be divided into classes in terms of the percentage of masculine or feminine tissue in the gonad. Individuals with more than 50 per cent of the tissue of their gonads consisting of masculine reproductive cells, showing spermatogenesis, are designated as hermaphroditic males and those with less than 50 per cent of the contents of their gonads made of male reproductive cells are called hermaphroditic females. On this percentage basis the gonads can be arranged from extreme masculine to pronounced feminine types.

Gonads of individuals which are classified as hermaphroditic males are shown in Fig. 2, *C* and *D*. Figure 2, *C* shows the gonad of a mature hermaphroditic male with more than 75 per cent of its reproductive tissues consisting of masculine cells. This gonad occurred in a *Limacina* 1.2 mm. in diameter. In contrast to the "pure male" type of gonad, a peripheral layer of ovarian tissue is present, but it amounts to less than 25 per cent of the total reproductive cells in the organ. In the medullary portion clusters of mature spermatozoa are present while in the cortical region a small number of egg cells are developing. Individuals possessing this type of gonad may be of any size but most of them are comparatively small. They are smaller than the pronounced feminine type but larger than the "pure males."

Figure 2, *D* shows the ovotestis of an individual belonging to the class having one-half to three-quarters of the gonad occupied by male tissue. In this ovotestis mature cells of both sexes are seen. At a point near the beginning of gonoduct, next to the retractor muscles, in the largest whorl of the spiral organ, mature ova and spermatozoa are seen ready to leave the sex gland. This simultaneous presence of ma-

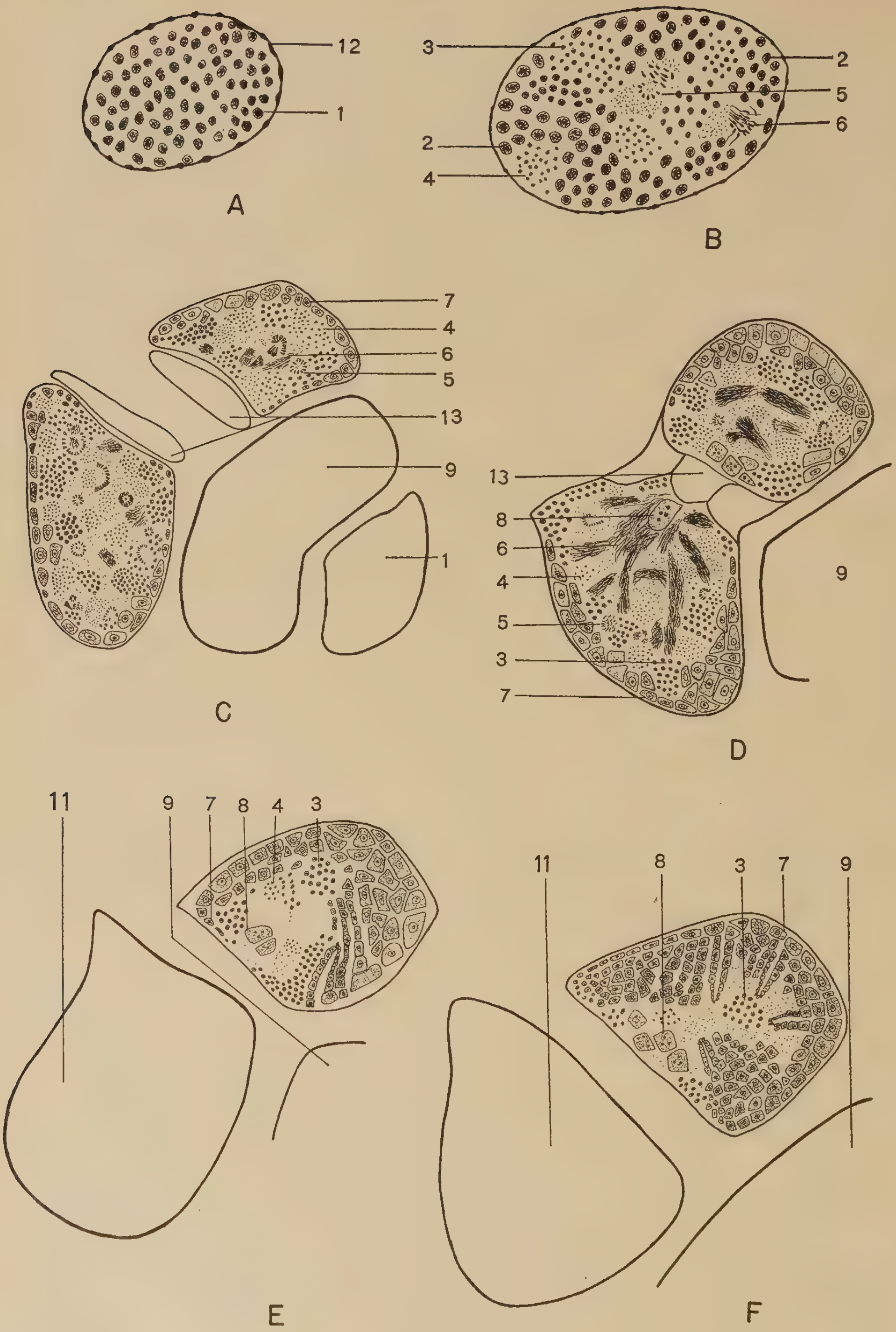

12
1
A
3
2
5
6
2
4
B
7
4
6
5
13
9
1
C
13
8
6
4
5
3
7
9
D
11
9
7
8
4
3
E
11
8
3
7
9
F

Figure 2

ture ova and spermatozoa near the gonoduct, or the presence of mature cells of both sexes along it, indicates that the animal is functioning both as male and female. Individuals of this type are called functional hermaphrodites, a name commonly used to designate this kind of reproductive individual among mollusks.

Animals with less than half of the gonadal tissues consisting of male reproductive cells, which are classified as hermaphroditic females, can also be divided into two groups in a similar manner: (*a*) hermaphroditic females with gonads containing 50–25 per cent of male tissue, and (*b*) hermaphroditic females with less than 25 per cent of male tissue in the gonad. These two types are represented in Fig. 2, *E* and *F*. As a general rule, gonads which are predominantly feminine are in a mature stage, containing mature ova and very often both mature ova and spermatozoa. The *Limacina* possessing these gonads are generally larger than the masculine types.

Part of a gonad with 25–50 per cent of its tissues consisting of male germ cells is shown in Fig. 2, *E*. This gonad is in a mature condition, for mature ova are found in the medullary portion of the ovotestis near the beginning of the gonoduct instead of in the cortical region where ovocytes of various stages of development are seen. Empty spaces are left in the gonad apparently by the spermatozoa which have vacated the

---

FIG. 2. Drawings of different types of gonads of *Limacina retroversa*.

A. Section of a complete gonad which is sexually undifferentiated.
B. A "pure male" gonad in which no ovocytes are seen—section of a complete gonad.
C. A hermaphroditic male gonad which has more than 75 per cent of its tissues made of male germ cells. Only the first or largest whorl is shown, the other two whorls being indicated by outlines.
D. First or largest whorl of a hermaphroditic male gonad with 50–75 per cent of its tissues consisting of male germ cells.
E. Right half of the first or largest whorl of a hermaphroditic female gonad which contains 25–50 per cent of male tissue.
F. Right half of the first or largest whorl of a hermaphroditic female gonad with less than 25 per cent of its tissues made of male germ cells.

1. Nucleus of pregerminative cell.
2. Nucleus of spermatogonium.
3. Primary spermatocytes.
4. Secondary spermatocytes.
5. Spermatids.
6. Spermatozoa.
7. Ovocyte.
8. Ovum.
9. Outline of second whorl of ovotestis.
10. Outline of third whorl of ovotestis.
11. Outline of left half of first whorl of ovotestis.
12. Fibrous connective tissue surrounding gonad.
13. Retractor muscles.

gonad previously. Figure 2, *F* shows a gonad which is even more predominantly feminine than that shown in Fig. 2, *E*. Less than 25 per cent of this ovotestis is made up of masculine reproductive cells.

In contrast to masculine types, the pronounced feminine hermaphro-

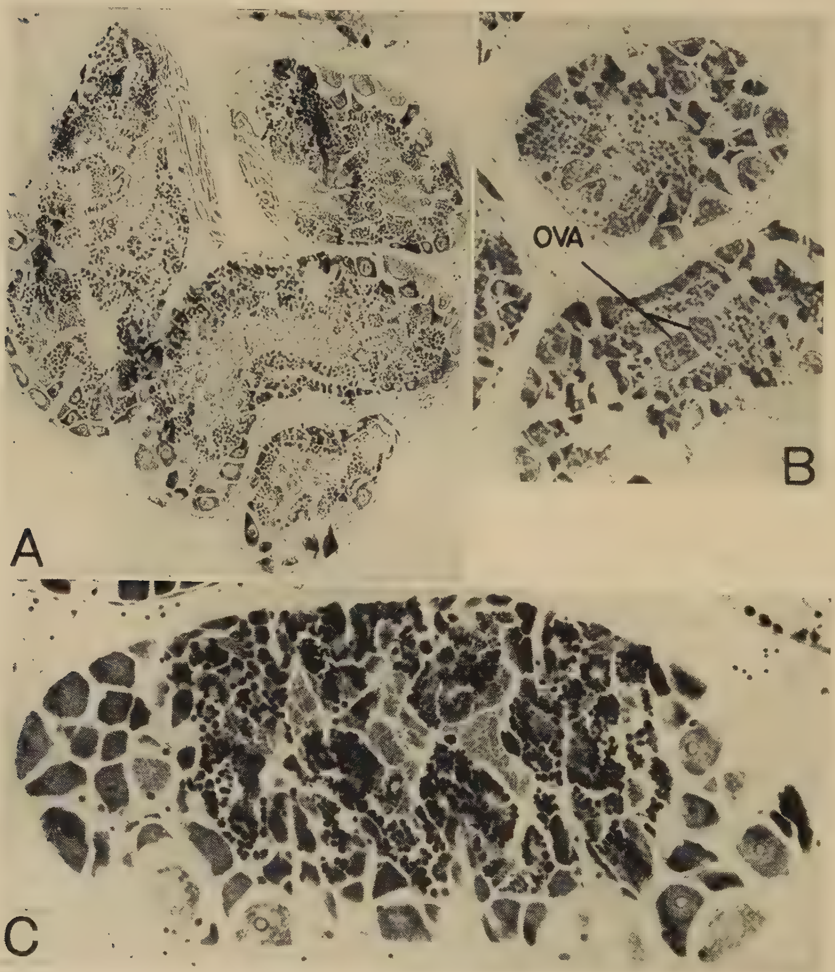


FIG. 3. Photomicrographs of sections of gonad of *Limacina retroversa*, showing hermaphroditic male and female gonads.

A. Hermaphroditic male gonad in which more than 75 per cent of the tissues consists of male reproductive cells.

B. Hermaphroditic female gonad in which 25–50 per cent of the gonadal tissues consists of male germ cells.

C. Further enlarged view of a section of the second whorl of a hermaphroditic male gonad with 50–75 per cent male tissue, showing the germ cells in greater detail.

dites possessing very little male tissue are limited to medium and, more generally, to large-sized *Limacina*. Another difference between the extremely male and female types is that while " pure males " are common, forming about one-half of the protandric males, " pure females " have never been observed. All female *Limacina retroversa* are hermaphroditic.

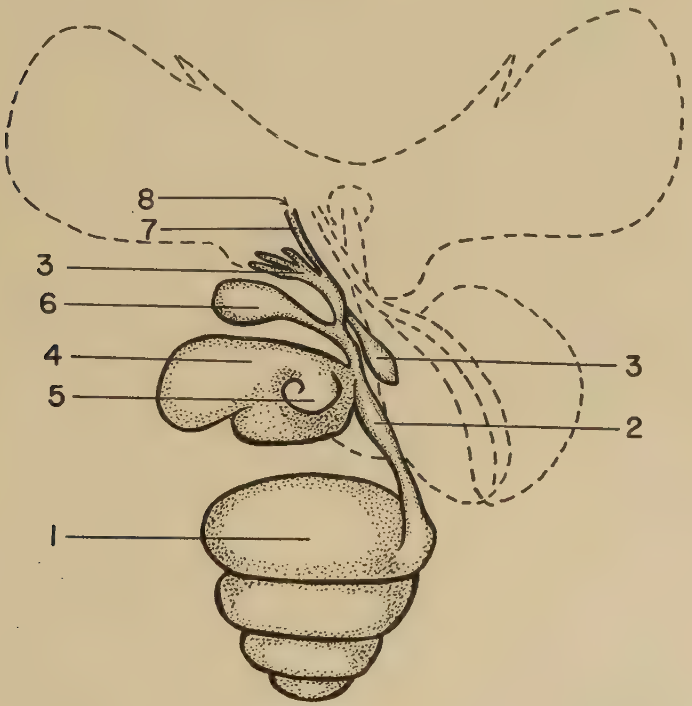


FIG. 4. Diagram of the reproductive system of *Limacina retroversa.*

1. Ovotestis.
2. Hermaphroditic duct or gonoduct.
3. Receptaculum seminis.
4. Shell gland.
5. Albumin gland.
6. Vesicula seminalis.
7. Out-going duct.
8. Genital opening.

Figure 3 shows some of the photomicrographs of sections of the gonad of *Limacina* upon which the diagrammatic drawings of Fig. 2 are based. Figure 3, *A* is a hermaphroditic male gonad with more than 75 per cent of its tissues consisting of male germ cells and Fig. 3, *B,* a hermaphroditic female gonad with 25–50 per cent of male tissue in it. Figure 3, *C* is a further enlarged view of a masculine gonad with

50–75 per cent male tissue showing the arrangement of the germ cells in greater detail.

The Accessory Organs of Reproduction.—The accessory organs of the reproductive system are diagrammatically represented in Fig. 4, which is a composite picture based upon the reconstruction from serial sections of the whole animal such as those shown in Fig. 5.

The gonoduct begins as a hermaphroditic duct for the passage of both ripe spermatozoa and ova. It opens into the ventral side of the anterior end of the spiral ovotestis and then turns to the right and passes forward, along the right side of the digestive track, to the anterior end of the body. It begins as a single tube with its wall composed of cuboidal cells, but later branches out into a pear-shaped structure (called "6" in Figs. 4 and 5). After meeting the accessory glands the gonoduct continues as the out-going duct. This part of the duct is much convoluted, leading to the external opening of the reproductive system on the right side of the mouth (8 in Fig. 4). This tube is composed of cuboidal epithelial cells with prominent nuclei and the cytoplasm of these cells contains a large quantity of secretory granules.

The accessory glands, like those of other pteropods, are very complicated structures. The largest gland, according to the terminology of Meisenheimer, is the shell gland. It is divided into three or four lobes occupying a great portion of the right side of the anterior part of the body of the animal. It opens into the hermaphroditic duct as well as the albumin gland (see Fig. 5, *D* and *E*). The shell gland is composed for the most part of large secretory cells, and tall, ciliated, columnar cells. The secretory cells are very abundant and obvious and with nuclei which are generally large and ellipsoidal, lying on the base of the cells away from the lumen of the gland, while the portion near it is filled with secretion. Perhaps the ovum stays longest in this gland on its way through the various parts of the reproductive system, for ova have been more often observed in this organ than in the others.

The albumin gland (Fig. 5, *B* to *D*) is a snail-like coiled gland associated with the shell gland but smaller than it. A diagram of its outline is shown in Fig. 4. The cells of the albumin gland are largely secretory. Their inner edge, which faces the lumen, is filled with transparent secretion when seen in sections stained with iron haematoxylin.

The vesicular seminalis (Figs. 4 and 5) is an elongated, pear-shaped organ connected with the hermaphroditic duct. It is lined with cuboidal epithelial cells. Inside this organ masses of mature spermatozoa are seen in the case of mature *Limacina.*

The receptaculum seminis is connected with the basal portion of the out-going duct. It consists of two portions. The first portion is much

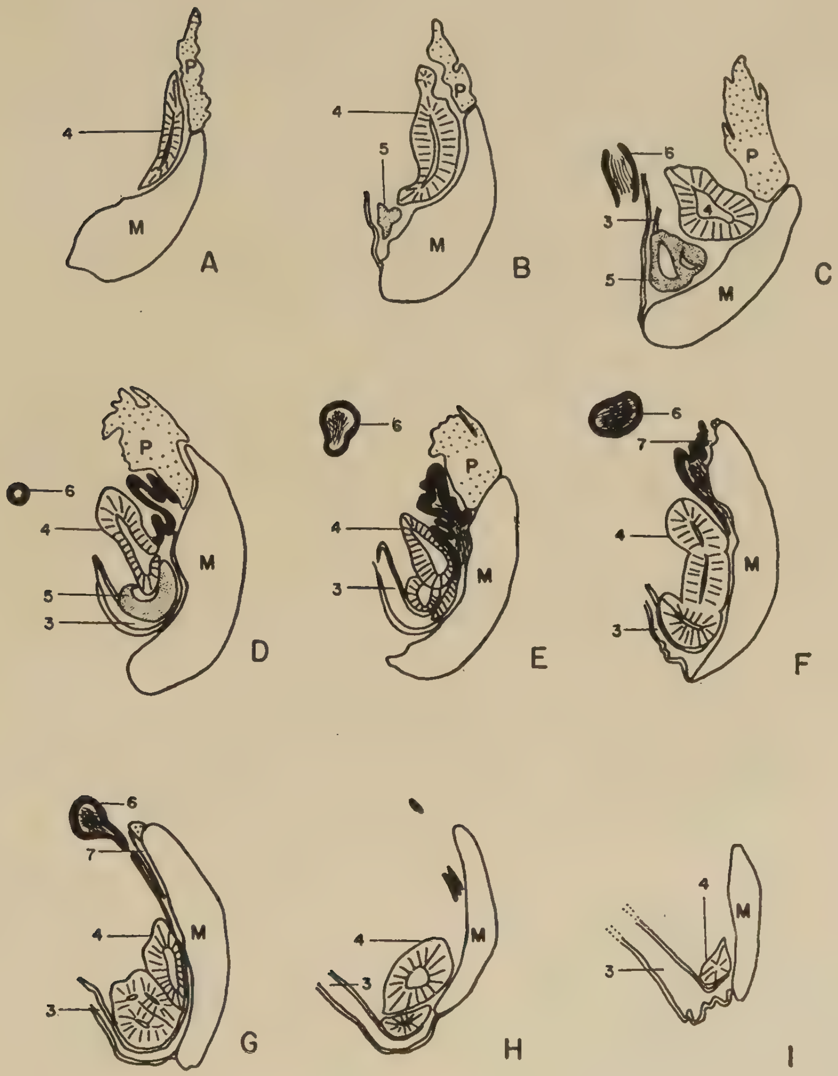

P
4
M
A
P
4
5
M
B
6
P
3
4
5
M
C
P
6
4
M
5
3
D
6
P
4
3
M
E
6
7
4
M
3
F
6
7
4
M
3
G
4
M
3
H
4
M
3
I

FIG. 5. Diagrams of longitudinal sections of the accessory organs of the reproductive system of *Limacina retroversa* (based upon camera lucida tracings from an animal cut into serial sections which are 5 micra thick).

Figure	Section No.
A.	90.
B.	100.
C.	115.
D.	124.
E.	135.
F.	155.
G.	165.
H.	175.
I.	195.

M. Mantle gland.
P. Penis (in Figs. *A–G*).
3. Receptaculum seminis (Figs. *C–I*).
4. Shell gland (in all the figures).
5. Albumin gland (Figs. *B–D*).
6. Vesicula seminalis (Figs. *C–G*).
7. Out-going duct (Figs. *F* and *G*).

folded, with a thick wall composed of columnar cells, while the second portion is much thinner, being made of cuboidal cells and baggy in appearance (Figs. 4 and 5). Spermatozoa observed in the folded portion stain deeply with iron haematoxylin and are normal in structure, but those within the second portion stain only very lightly with the same

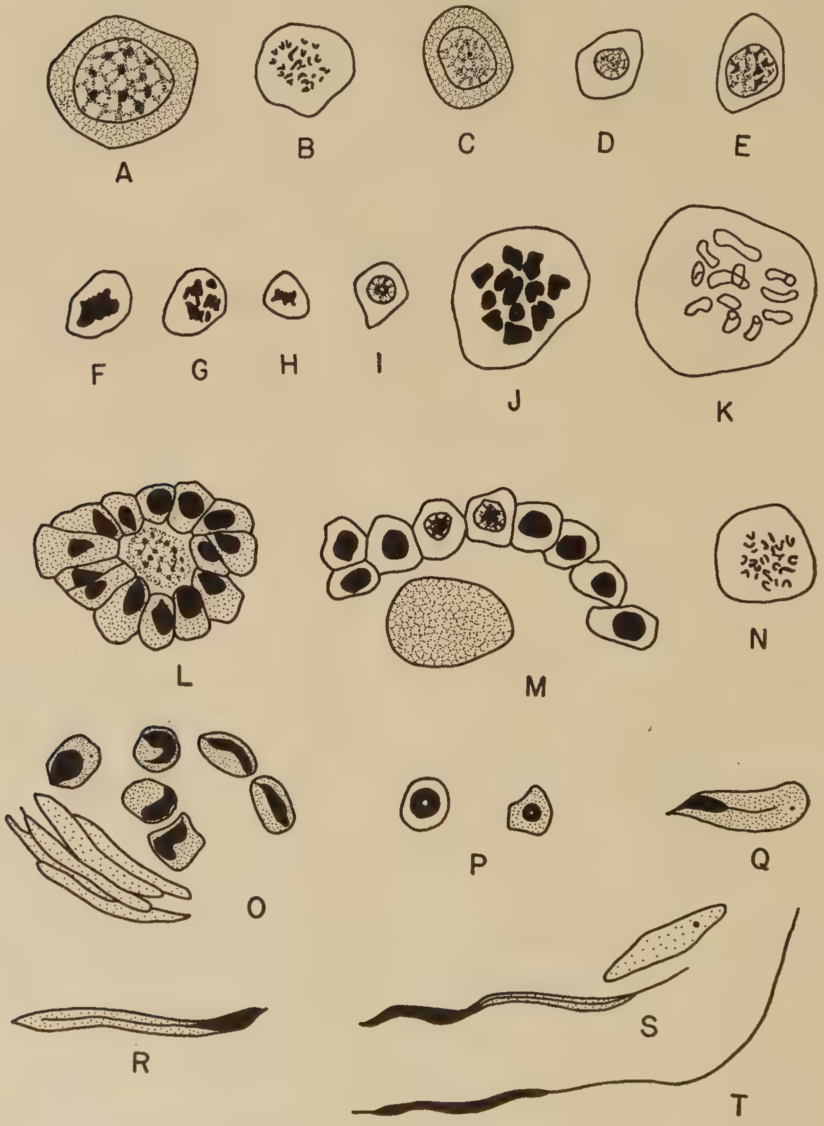


FIG. 6. Spermatogenesis of *Limacina retroversa*.

dye and show signs of degeneration and masses of disintegrating material are often observed.

The penis is practically independent of the rest of the reproductive system both in position and in structure. In well-developed adults it is a very large organ lying dorsad to the rest of the genital structures in the anterior portion of the body near the mantle gland (*P* in Fig. 5). This organ is very much folded on its outer surface when not distended. It has its own secretory glands and retractor muscles. The spermatozoa which come out of the gonoduct run along the ciliated seminal groove towards the penis along the right side of the dorsal region of the " fin " or " flapper."

General Features of Gametogenesis

The development of the male and female reproductive cells has been examined from fixed material cut into serial sections and stained with iron haematoxylin as well as from fresh specimens treated with the carmine smear technique. The steps in spermatogenesis have been ascertained, and it has been found that the maturation of the male germ cells is essentially the same as that of other gastropods.

The pregerminative cells grow and multiply to form the primary spermatogonia (Fig. 6, *A*). The primary spermatogonia (Fig. 6, *B*)

EXPLANATION OF FIGURE 6

A. Primary spermatogonium.
B. Metaphase plate of primary spermatogonium showing the diploid number of 24 chromosomes.
C. Secondary spermatogonium.
D. Primary spermatocyte, beginning of leptotene threads.
E. Primary spermatocyte, showing tetrad condition.
F. Metaphase of first meiotic division, profile.
G. Polar view of anaphase of first meiotic division.
H. Early anaphase of second meiotic division, profile.
I. Young spermatid.
J. Chromosome plate of early anaphase of first meiotic division showing the haploid number of 12 chromosomes.
K. Chromosome plate of early anaphase of second meiotic division, showing 12 chromosomes.
L. A group of spermatids around a central cell.
M. Same as *L,* with spermatids not completely enclosing the central cell.
N. Metaphase plate of a somatic cell, showing the diploid number of 24 chromosomes.
O. Separate spermatids undergoing nuclear elongation, besides them a mass of discarded cytoplasm from other older spermatids.
P. Cross-sections of spermatids showing the central canal.
Q. Elongated spermatid, showing formation of tail filament.
R. Spermatid further elongated than *Q.*
S. Nearly mature spermatozoön with discarded cytoplasm beside it.
T. Mature spermatozoön.

divide by mitosis to give rise to the secondary spermatogonia (Fig. 6, *C*) which are smaller in size and with a higher nucleus-cytoplasm ratio than the primary. Generally the nucleus is placed on one side of the cell. Figure 6, *B* is a metaphase plate of a primary spermatogonium showing 24 chromosomes. The secondary spermatogonia differentiate into primary spermatocytes by mitosis. The primary spermatocytes are identified by the fact that they are nearly always grouped together in the gonad. At the first meiotic division the chromatin of the primary spermatocyte breaks up and forms loose masses and then changes into leptotene threads. These threads, as in some pulmonates, for example, *Succina ovalis, Ostrea lurida,* form such a compact mass that it is difficult to follow the steps in conjugation and tetrad formation (that is, parasynapsis and diakinesis). Figure 6, *D* shows the beginning of the leptotene threads with the nucleolus still visible and Fig. 6, *E* shows a protetrad condition of the chromatin material after parasynapsis. The tetrads of early diakinesis in the form of circles and crosses are arranged on the surface of the nuclear membrane and take a very dark color in staining. A profile of the metaphase of the first meiotic division is shown in Fig. 6, *F,* while Fig. 6, *G* is a polar view of the anaphase of the same division. Figure 6, *J* is a much enlarged polar view of the early anaphase of this division showing the reduced number of 12 chromosomes. During telophase the chromosomes draw together and form a compact mass in the secondary spermatocytes.

From the fact that a resting stage of the secondary spermatocyte is not seen it is inferred that this stage is most probably absent. This situation has been reported by Furrow (1935) for *Valvata tricarinata.* Cells undergoing the second meiotic division are smaller in size than those of the first. Figure 6, *H* is a profile of the early anaphase of the second meiotic division, and Fig. 6, *K* is a much enlarged view from one pole of the chromosome plate at an early anaphase of this division showing the haploid number of twelve chromosomes. During the telophase of this division the chromatin material becomes reticular as the nuclear membrane reappears and later condenses into a very dark staining structure which eventually becomes the dark nucleus of the spermatid. In Fig. 6, *I* a newly-formed nucleus of a younger spermatid is shown. Two of the spermatids of Fig. 6, *M* are also in this condition. These figures show the formation of reticular structures within the nuclear membrane and the condensation of the chromatin material in forming the dense nucleus of the spermatid.

The spermatids are generally arranged around a large degenerating cell which may be homologized with the " nurse cell " reported in most mollusks, but no cytoplasmic connection between it and the spermatids has been observed (Fig. 6, *L* and *M*). In spermiosis the darkly-staining nucleus elongates first at one point so as to assume an acutely ovate outline (Fig. 6, *L*). A few of the various shapes assumed by the nucleus during its metamorphosis into the head of the mature spermatozoön are shown in Fig. 6, *O*. In association with the change of the nucleus, the cytoplasm elongated and the axial filament of the tail-piece appears (Fig. 6, *Q*). In the cross-section of an old spermatid of this stage the central canal through the nucleus can be seen as a light area in the center (Fig. 6, *P*). The spermatid is transformed into a mature spermatozoön by further elongation of the cytoplasm together with the growth of the axial filament and lengthening of the nucleus followed by a discarding of a greater portion of the cytoplasm (Fig. 6, *Q* to *S*). The head-piece of the spermatozoa is slender and pointed at the anterior end. It is formed by the nucleus. The tail-piece consists of an axial filament and a very slender tail membrane formed by the cytoplasm. The middle piece of the spermatozoön is not clearly seen and its development could not be followed in our material. A mature spermatozoön (Fig. 6, *T*) is about 30 micra long and its head about half as long as its tail-piece. During spermiosis the spermatids move away from a spherical arrangement about a central " nurse cell " and become irregularly placed as seen by a comparison of Fig. 6, *L* and Fig. 6, *O*. When the spermatozoa are mature they are placed closely together side by side with their heads pointing in the same direction, but they do not form " sperm balls " or " sperm morulae." In no case has a " nurse cell " been observed to which the heads of the spermatozoa are attached as has been reported for some pulmonates and prosobranchiates.

In specimens used in this study no atypical spermatogenesis has been observed. The only element in the gonad which might suggest apyrene spermatozoa is that shown in Fig. 6, *O*. It consists of a mass of elongated, enucleated structures which stain very lightly. But it appears more probable that they are discarded portions of the cytoplasm of the transforming spermatids rather than apyrene spermatozoa for no steps comparable to the atypical spermatogenesis leading to the formation of these structures have been observed.

The diploid number of chromosomes is 24. This number was first deduced from observations on the secondary spermatocytes which exhibit the haploid number of 12 chromosomes and was again checked against the chromosome plates of somatic cells. A metaphase chromosome plate of a somatic cell drawn with a camera lucida from a carmine smear is shown in Fig. 6, *N* and it may be compared with the chromosome plate of the mitotic division of the spermatogonium shown in Fig. 6, *B*. The chromosome number was further confirmed by the chromosome plates of the second miotic division which also shows (Fig. 6, *K*) the haploid number of 12 chromosomes.

It has been observed in young gonads (Fig. 2, *B*) that there were at first only a few clusters of spermatozoa in the whole organ. As the animal grows the number of clusters of spermatozoa increases and eventually, in a mature *Limacina,* the mass of spermatozoa constitutes nearly all the male tissue in the gonad. It has been reported in other mollusks that each cluster of spermatozoa descends from one primary spermatogonium. If this is also the case in *Limacina,* then it appears from this gradual increase of the number of clusters of spermatozoa with the growth of the animal that the spermatogonia do not all develop at the same time, but that they follow each other in their maturation.

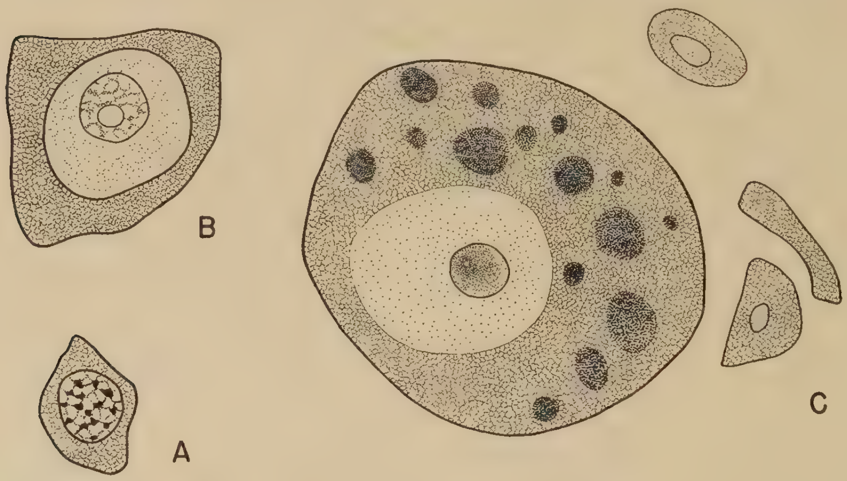


FIG. 7. Drawings of the female reproductive cells of *Limacina retroversa* (Fleming).

A. An oögonium.
B. A growing ovocyte with homogeneous cytoplasm.
C. A nearly mature ovum with a number of darkly-staining granules in the cytoplasm.

The female cells as a whole evidently develop slower than the male so that the animal generally assumes a protandric condition. The process of maturation of the female reproductive cells cannot be readily observed in our specimens of *Limacina retroversa.* When the different ovocytes in the ovotestis are compared it is seen that the growth of the cells is associated with the deposition in the cytoplasm of large granules which stain very dark with haematoxylin. The nucleus, on the other hand, takes stain less and less easily and eventually becomes much lighter as the ovocytes grow in size. A mature ovum measures 50 to 70 micra, which represents an increase of five to seven times in diameter over the first ovocyte. Figure 7 shows an oögonium together with a growing ovocyte and a nearly mature ovum. The change in size is quite noticeable.

As in the case of spermatogenesis, the ova do not all mature simultaneously, but only a few are fully developed at a time. When once started, oögenesis seems to continue throughout the remainder of life of the individual. Female germ cells before and during maturation are located on the peripheral region of the gonad, but ova, when mature, migrate to the central portion of the gonad and thence to the opening of the gonoduct (Figs. 2, *D* and 2, *E*). Fertilization probably takes place during the passage of the ova through the gonoduct.

Female reproductive cells of different ages are present in the gonad, but the maximal number of mature ova observed in a single five micra section of one whorl of the ovotestis is not greater than ten to twenty. The largest number of ova observed in the gonoduct at the time of fixation is about four or five. These observations, together with the fact that *Limacina retroversa* kept in the laboratory lay a few eggs at a time, indicate that this animal does not spawn out after a brief period of intensive reproductive activity, but that spawning is more or less protracted and continuous after it has once began.

Discussion and Summary

From the above description of the maturation of the germ cells of *Limacina retroversa* it will be seen that the process of spermatogenesis in this species agrees with those of other gastropod mollusks. Von Brunn (1884) first observed atypical spermatozoa and considered them to be rudimentary ova. Meves (1903) and Hertwig (1905), however, have described the steps in atypical spermatogenesis and tried to elucidate the morphological and physiological significance of this process and its product. Reinke (1914) in *Strobus bituberculatus* and Kuschakewitsch (1910, 1911) in *Conus* and *Vermetus,* Gould (1917) in *Crepidula plana,* and other authors, made similar studies. Recently Hickmann (1931) described atypical spermatogenesis in *Succina ovalis,* Furrow (1935) in *Valvata tricarinata,* Coe and Turner (1938) in *Mya arenaria.* But as far as it can be ascertained there is no atypical spermatogenesis in *Limacina retroversa.* This species seems to belong to the group of mollusks that do not show atypical spermatogenesis.

Nurse-cells have been reported in many forms of mollusks during their maturation, but in *Limacina retroversa* the arrangement of the spermatids and newly matured spermatozoa about a central cell may suggest the presence of nurse-cells though no cytological connection has been observed between these and the germ cells.

Mature spermatozoa form balls or " sperm morulae " (according to Orton, 1926) in certain mollusks while in others, though of the same genus, they do not. Thus, *Ostrea lurida* and *Ostrea virginica,* in this country, have clustered and separate mature spermatozoa respectively. *Limacina retroversa* have separate mature spermatozoa.

The accessory organs of the reproductive system of *Limacina retroversa* agree very closely with the description given by Meisenheimer, who did not mention which species were used as representatives of the genus *Limacina* in his comparative studies. However, if Meisenheimer's work on the secondary sexual organs is taken as a typical description of the genus *Limacina,* then *Limacina retroversa* may be considered as closely resembling the typical forms in the structures of the accessory sexual organs.

BIBLIOGRAPHY

Bigelow, H. B., 1926. Plankton of the off-shore waters of the Gulf of Maine. *Bull. U. S. Bur. Fish.,* **40** (Part II): 1 (1924).

Bonnevie, K., 1916. Mitteilung über Pteropoden. L. Beobachtungen über den Geschlechtsapparat von Cuvierina columnella Rang. *Jena Zeitschr. Nat.,* **54**: 245.

Bourne, G. C., 1889. The generative organs of the oyster. (Abstract of a paper by Dr. P. P. C. Hoek.) *Jour. Mar. Biol. Ass'n,* **1**: 268.

Coe, W. R., 1931. Spermatogenesis in the California oyster (O. lurida). *Biol. Bull.,* **61**: 309.

Coe, W. R., 1933. Sexual phases in Teredo. *Biol. Bull.,* **65**: 283.

Coe, W. R., and H. J. Turner, Jr., 1938. Development of the gonads and gametes in the soft-shell clam (Mya arenaria). *Jour. Morph.,* **62**: 91.

Fleming, J., 1823. On a reversed species of Fusus (Fusus retroversus). *Mem. Werner. Soc.,* **4**: 498.

Fol, H., 1874. Note sur le développement des Mollusques Ptéropodes et Cephalopodes. *Arch. d. Zool. Expér. et Gén.,* **3**: 33.

Fol, H., 1875. Études sur le développement des mollusques. I. Sur le développement des ptéropodes. *Arch. Zool. Expér. et Gén.,* **4**: 1.

Furrow, C. L., 1935. Development of the hermaphrodite genital organs of Valvata tricarinata. *Zeitschr. f. Zellforschung.,* **22**: 282.

Gegenbaur, C., 1853. Bau der Heteropoden u. Peteropoden. *Zeitschr. f. wiss. Zool.,* **4**: 334; 369.

Gegenbaur, C., 1855. Untersuchungen über Pteropoden u. Heteropoden. Ein Beitrag zur Anatomie u. Entwicklungsgeschichte dieser Thiere. Leipzig.

Gould, H. N., 1917. Studies on sex in the hermaphrodite mollusc (Crepidula). I. History of sex cycle. *Jour. Exper. Zool.,* **23**: 1.

Hertwig, R., 1905. Über das Problem der sexuellen Differenzierung. *Verh. deutsch. Zool. Ges.,* **15**: 186.

Hickman, C. P., 1931. Spermatogenesis of Succinea ovalis Say, with special reference to the components of the sperm. *Jour. Morph. and Physiol.,* **51**: 243.

Knipowitsch, N., 1891. Zur Entwicklungsgeschichte von Clione limacina. *Biol. Centralbl.,* **11**: 300.

Krohn, A., 1856. Beobachtungen aus der Entwicklungsgeschichte der Pteropoden, Heteropoden und Echinodermen. *Müller's Arch. f. Anat.*, p. 515.

Kuschakewitsch, S., 1910. Zur Kenntnis der sogenannten warmförmigen spermien der Prosobranchier. *Anat. Anz.*, **37**: 318.

Kuschakewitsch, S., 1911. Über die Entwicklung der spermien bie Conus mediterraneus Brug. und vermatus gigas Biv. *Biol. Centralbl.*, **31**: 530.

Loosanoff, V. L., 1937. Development of the primary gonad and sexual phases in Venus mercenaria L. *Biol. Bull.*, **72**: 389.

Meisenheimer, J., 1905. Pteropoda. *Wiss. Ergebn. de Deutsch, Tiefsee Exp., Valdivia*, 9.

Meves, F., 1903. Ueber oligopyrene und apyrene spermien und ihre Entstehung nach Beobachtungen an Paludina und Pygaera. *Arch. f. micros. Anat.*, **61**: 1.

Müller, J., 1858. Sur le développement des Pteropoden. *L'Institute*, **26**: 37.

Orton, J. H., 1909. On the occurrence of protandric hermaphroditism in the mollusc Crepidula fornicata. *Proc. Roy. Soc., B*, **81**: 468.

Orton, J. H., 1926. Observations and experiments on sex-change in the European oyster (O. edulis). *Jour. Mar. Biol. Ass'n*, **14**: 967.

Reinke, E. E., 1912. A preliminary account of the development of the apyrene spermatozoa in Strombus and of the nurse-cells in Littorina. *Biol. Bull.*, **22**: 319.

Reinke, E. E., 1914. The development of apyrene spermatozoa of Strombus bituberculatus. *Carnegie Inst. Washington*, Publ. No. 183, p. 195.

Souleyet, L., 1843. Observations anatomiques, physiologiques et zoologiques sur les mollusques ptéropodes. *Compt. Rend. Acad. Sci.*, **17**: 662.

Stephan, P., 1903. Sur les spermies oligopyrènes et apyrènes de quelques Prosobranches. *Compt. Rend. Soc. Biol., Paris*, **55**: 554.

Tesch, J. J., 1913. Pteropoda. Das Tierreich, 36.

Thiele, J., 1931. Handbuch der Systematischen Weichtierkunde.

Van Beneden, P. J., 1839. Memoire sur la Limacina arctica. *Nouv. Mém. Acad. Roy. Sci. et Belles Lettres de Bruxelles*, T. 14.

Von Brunn, M., 1884. Untersuchungen über die doppelte Form der Samenkörper von Paludina vivipara. *Arch. Mikrosk. Anat.*, **23**: 413.

Zarnik, B., 1911. Über den Chromosomencyclus bei Pteropoden. *Verh. deutsch. Zool. Ges.*, Leipzig, **20**: 205.

Contribution No. 199

REPORTS ON THE SCIENTIFIC RESULTS OF THE FIRST ATLANTIS EXPEDITION TO THE WEST INDIES, UNDER THE JOINT AUSPICES OF THE UNIVERSITY OF HAVANA AND HARVARD UNIVERSITY

Preliminary Descriptions of One New Genus and Seventeen New Species of Decapod and Stomatopod Crustacea *

BY FENNER A. CHACE, JR.
Museum of Comparative Zoölogy.

The final reports on the results of these expeditions will contain complete descriptions and figures of the following species.

Family Pasiphaeidae

Pasiphaea poeyi, sp. nov.

Holotype.—Male, M.C.Z. No. 10237, Bahia de Cochinos, Santa Clara Province, Cuba, Lat. 22° 07′ N., Long. 81° 08′ W., 220-275 fathoms, February 25, 1938; station 2963-D.

Paratypes.—Ovigerous female, Nicholas Channel north of Santa Clara Province, Cuba, Lat. 23° 16′ 30″ N., Long. 80° 11′ W., 415 fathoms, March 14, 1938; station 2990-A.

Female, off Bahia Cardenas, Matanzas Province, Cuba, Lat. 23° 24′ N., Long. 81° 00′ 30″ W., 370-605 fathoms, March 16, 1938; station 2995.

Carapace about as long as the first three abdominal somites, not carinate dorsally except on the gastric tooth. The latter does not reach quite as far as the anterior margin of the carapace. Branchiostegal sinus very shallow, merely forming a sinuous outline to the anterolateral margin of the carapace; the branchiostegal spine arises from the margin of the carapace. Abdomen with no trace of a carina

---

* Contribution No. 199 of the Woods Hole Oceanographic Institution.

on the first three somites; fourth, fifth and sixth somites somewhat flattened dorsally making an obtuse angle with the lateral surfaces. Hinder margin of sixth somite evenly rounded off without any spine or sharp projection. Telson about three-fifths as long as sixth segment and very faintly grooved dorsally on the proximal half, then the groove disappears completely and finally reappears again, becoming very distinct at the distal end. Tip of telson nearly transverse, slightly convex either side of a shallow median sinus; the emargination is deeper in the ovigerous female, but still quite shallow. Basal joint of antenna with an inferior spine; the antennal scale is slightly less than half as long as the carapace, the blade narrowly truncate, not broadly rounded at the end. Third maxillipeds fall short of the end of the antennal scale. First two pairs of legs nearly equal in lenght, the second reaching slightly farther than the first, both pairs overreach the tip of the antennal scale by about half the length of the fingers. Both first and second legs have a strong spine on the basis and another on the ventral distal angle of the carpus, that of the second pair being much the stronger. The merus of the first leg is unarmed, that of the second with a single ventral spine at about the end of the proximal third. Fingers of the first chela about three-fourths as long as the palm, those of the second slightly longer than the palm.

Measurements.—Total length of holotype about 51 mm., carapace 14.7 mm. The ovigerous female paratype has a carapace length of 22.2 mm. and the non-ovigerous female a carapace length of 21.2 mm.

This species seems to show the closest affinities with *P. americana* Faxon, *P. cristata* Bate, *P. flagellata* Rathbun, *P. kaiwiensis* Rathbun, *P. unispinosa* Wood-Mason and *P. merriami* Schmitt. *P. americana* differs by having the telson more strongly notched, the branchiostegal sinus very deep and a spine at the middle of the lówer margin of the merus of the second legs. *P. cristata* has the gastric spine of different form and apparently no spine on the basis of the first and second legs. *P. flagellata* has the telson longer and grooved for the entire length and the meri of the first legs multispinose. In *P. kaiwiensis* the branchiostegal sinus is more pronounced and the merus of the second legs multispinose. According to Schmitt, *P. unispinosa* has the carapace sharply carinate for most of its dorsal margin. Finally, *P. merriami* has a much more pronounced branchiostegal sinus, the spine on the merus of the second legs at the distal third and the third maxillipeds and first two pairs of legs proportionately longer.

Parapasiphaë macrodactyla, sp. nov.

Holotype.—Female, M.C.Z. No. 10238, S.S.E. of Bahia de Guantanamo, Oriente Province, Cuba, Lat. 19° 40′ N., Long. 75° 03′ W., 1920 fathoms, March 5, 1938; station 2968.

Carapace dorsally sharply carinate for practically its entire length the carina becoming rather high and thin on the gastric region. There are no spines on the lateral portions of the carapace near the anterior margin and the branchiostegal sinus is rounded, not quite semicircular. A ridge starting behind the antennae runs somewhat downward subparallel to the lower margin of the carapace as far as the branchial region where it forks, the lower branch passing horizontally backward nearly to the posterior margin, the upper branch passing diagonally upward toward the posterior end of the upper margin of the carapace, but curving downward again before going much more than halfway and disappearing before reaching the hind margin. Another short, sinuous ridge arises behind the antennules and passes diagonally downward, but disappears before reaching the postantennal ridge. Rostrum slants somewhat downward, reaching as far as the middle of the cornea where it terminates in a narrow, somewhat truncate tip armed at the upper angle with a prominent spine. There is a spine arising from the dorsal carina at about the end of the proximal third of the rostrum and a vestige of a second spine about in line with the posterior margin of the orbits. Abdomen not carinated on the first three somites, although the posterior portion of the third is obscurely angulate dorsally. Fourth segment ends in a broadly triangular tooth, sharply carinated in the midline, which overhangs the fifth segment. The latter is broadly flattened dorsally. The sixth is smoothly rounded. Telson nearly half again as long as sixth somite, dorsally sulcate for its entire length and armed terminally with nine spines, of which the outer pair is much the largest. Eyes of the form usual in the genus; width of cornea about half the length of the eyestalks from the base to the cornea. Antennular peduncle stout, extending to about the middle of the antennal scale; stylocerite broad, the terminal spine directed outward. Antennal peduncle with a spine belov the base of the scale. The latter is between one-third and two-fifths as long as the carapace and rostrum, rather narrowly truncate distally with a prominent distal spine. Third maxillipeds extend beyond the antennal scale by about one-third the length of the terminal segment. First pereiopods extend beyond the antennal scale by all but the proximal fourth of the palm. There is a spine on the basis, one stout spine in the distal half and several stout setae on the lower margin of the merus, a sharp angle at the lower distal end of the carpus and several setae but no spines on the hand. Palm somewhat triangular in cross section and about one-third longer than the fingers; the latter are slender and cross for some distance at the tip. Second legs extend beyond the first by about half the length of the fingers. They are armed with a ventral terminal spine on the basis, a single spine on the lower margin of the ischium, five spines and several setae on the lower margin of the merus, a very strong compressed spine at the lower angle of the carpus and several spinules or stout setae on the hand. The slender fingers are between a fifth and a fourth again as long as the palm and they cross at the tips like the first pair. The third legs reach almost to the middle of the palm of the second pair. The fourth extend about to the middle of the merus of the third. And the fifth pair are longer than the fourth, extending about to the distal third of the merus of the third pair.

Measurements.—Total length about 71 mm.; length of carapace and rostrum 24.8 mm.; length of rostrum 3.0 mm.; length of antennal scale 9.3 mm.; length of palm of first leg 6.9 mm.; length of fingers of first leg 5.2 mm.; length of palm of second leg 8.1 mm.; length of fingers of second leg 9.9 mm.

The form of the rostrum, the absence of lateral spines on the carapace and, particularly, the length of the fingers of the second pair of legs serve to distinguish the present species from all previously described forms.

Family Bresiliidae

Lucaya, gen. nov.

Similar to *Bresilia* Calman (Trans. Royal Irish Acad., vol. 31, pt. 1, 1896, p. 7) except that there are exopods on all five pairs of pereiopods rather than only on the first two pairs and the gill series is made up of five pleurobranchs, the one above the last legs being well-developed rather than vestigial.

The genus name is derived from *Lucayos,* the original name of the Bahama Islands.

Lucaya bigelowi, sp. nov.

Holotype.—Male, M.C.Z. No. 10239, east of Great Abaco Island, Bahamas, Lat. 26° 12′ N., Long. 76° 26′ W., 2610 fathoms, January 29-30, 1938; station 2946.

Integument pitted or coarsely punctate. Carapace short and broad, dorsally carinated in the anterior half by the prolongation of the rostral carina and armed with a strong spine at the lower angle of the orbit but without any trace of a spine below this, the anterolateral angle being smoothly rounded. Rostrum curved slightly downward, robust, supported by a stout lateral carina continuous with the posterior margin of the orbit. In cross section the rostrum would appear nearly quadrate due to its breadth at the lateral carinae. It extends as far as the end of the antennular peduncle and is armed dorsally with twelve small, closely set, subequal teeth; the ventral margin is unarmed. Abdomen without trace of a carina or armature of any kind, although the third segment is produced over the fourth in a curious hood-like manner as in *Bresilia atlantica* Calman. Telson somewhat shorter than the sixth abdominal somite and armed with two pairs of dorsolateral spinules situated in the posterior half, and eight terminal spines of which the next to the outer pair are the strongest. Eyes extend slightly beyond the mid-point of the rostrum when turned forward; the cornea is dark brown in color and but little wider than the stalk upon which it is set rather obliquely. Antennular peduncle stout, the second and third segments subequal in length. Lamina of antennal scale more sharply angular and extending even farther beyond the outer spine than in *B. atlantica.* First pair of pereiopods somewhat more robust than the second and little, if any, shorter. Last three legs not very long and decreasing in length progressively from the third to the fifth; the ischial and meral joints of the third and fourth legs are armed with a few long spines.

Measurements.—Total length about 19 mm.; length of carapace and rostrum 7.0 mm.; length of rostrum 2.7 mm.

Aside from the generic characters, this species differs from *Bresilia atlantica* Calman (Calman; Trans. Royal Irish Acad., vol. 31, pt. 1, 1896, p. 7, pl. 1, figs. 1-14, pl. 2, figs. 15-18, *and* Kemp; Fisheries Ireland, Sci. Invest., 1908, No. 1 (1910), p. 82, pl. 10, figs. 1-7) as follows. There is no spine at the anterolateral angle of the carapace. The rostrum reaches as far as the end of the third antennular segment instead of nearly to the end of the second, is somewhat curved downward rather than horizontal or even slightly concave dorsally and has twelve dorsal teeth and none below rather than three to four dorsal and two to four ventral. The telson has two pairs of dorsolateral spinules instead of six to eleven, and eight terminal spines of which the next to the outermost are largest instead of twelve with the outer pair the largest; the telson is somewhat shorter in proportion to the sixth abdominal somite. The eyes are well pigmented and set obliquely on their stalks. The antennular peduncle is shorter and stouter, the second segment being subequal in length to the third rather than twice as long. Finally, the last three pereiopods are much shorter and decrease rather than increase successively in length posteriorly.

This species is named for Dr. Henry B. Bigelow, Curator of Oceanography in the Museum of Comparative Zoölogy, whose efforts were instrumental in the success of the present expedition.

Family Psalidopidae

Psalidopus barbouri, sp. nov.

Holotype.—Ovigerous female, M.C.Z. No. 10240, Nicholas Channel south of Cay Sal Bank, Lat. 23° 21′ N., Long. 79° 58′ W., 300-315 fathoms, March 13, 1938; station 2987-C.

Integument form, everywhere hispid. Carapace armed with a median dorsal row of long spines, another row starting at the base of the rostrum and pursuing a slightly sinuous course above the branchial region to the hind margin and a second lateral row below the branchial region; this last sub-branchial row is not quite continuous with a row passing backward from the anterior margin behind the antenna as far as the branchial region. The only other distinct spines on the carapace are one just below the lower angle of the orbit on the anterior margin, one at the anterolateral angle and one or two on the posterior edge of the branchial region between the ends of the supra-branchial and sub-branchial rows. Rostrum a little more than half again as long as the carapace, ascendant and nearly straight until just behind the tip where it turns a little more strongly upward. It is armed with four rows of spines, dorsal, ventral and lateral, of which the dorsal and ventral are made up of spines about twice as long as those of the lateral. Abdomen with a mid-dorsal row of spines on each of the first six somites and several spines on the lateral portions and on the borders of the pleurae very much as in *P. huxleyi* Wood-Mason. Telson densely hispid dorsally. The appendages are almost identical with those of *P. huxleyi.* The holotype carries about a dozen large eggs.

Measurements.—Total length 115.7 mm.; length of carapace 22.6 mm.; length of rostrum 35.7 mm.; length of abdomen 61.0 mm.

In the present collection, from nearly the same locality, is a smaller female specimen about 68 mm. long which agrees with the holotype in practically every particular except that there is a long, needlelike spine on the last thoracic and all of the abdominal sternites much as in *P. spiniventris* Wood-Mason. It therefore seems likely that the ventral spines in this genus are either individual variations or are evidences of immaturity, as might be deduced from the fact that the two known specimens of *P. huxleyi* are larger than any one of the five or six specimens of *P. spiniventris* so far discovered. Whichever is the explanation, it seems safe to assume that there is but one Indo-Pacific species, P. *huxleyi*, of which *P. spiniventris* now becomes a synonym. The Atlantic species differs only in having a shorter, straighter rostrum and the lateral spines of the carapace confined almost entirely to but two longitudinal rows.

This species is named for Dr. Thomas Barbour, Director of the Museum of Comparative Zoölogy, who is largely responsible for making the present expedition possible.

Family Pandalidae

Plesionika macropoda, sp. nov.

Holotype.—Male, M. C. Z. No. 10241, Bahía de Cochinos, Santa Clara Province, Cuba, Lat. 22° 07′ N., Long. 81° 08′ W., 195-235 fathoms, February 23, 1938; station 2961-D.

Paratypes.—A male from the same station.

Female, Old Bahama Channel, due north of Punta Alegre, Camagüey Province, Cuba, Lat. 22° 48′ N., Long. 78° 48′ W., 220-225 fathoms, March 10, 1938; station 2980-B.

Carapace dorsally carinate on the anterior two-thirds and armed on the anterior margin with a strong antennal spine and a somewhat smaller branchiostegal spine. Rostrum nearly twice as long as carapace, descendent in its proximal third and then ascendant and nearly straight from that point to the apex. The rostral crest is armed with two or three movable and five fixed spines, of which the movable and the proximal one of the fixed spines are behind the orbit; beyond the end of the antennular peduncle the dorsal margin of the rostrum is unarmed. The ventral margin bears eleven subequally spaced teeth. Abdomen smoothly rounded dorsally, the third segment produced posteriorly but the angle formed is obtuse, not acute. The sixth somite is a little more than twice as long as the fifth and very little longer than the telson. Telson armed with four pairs of dorsolateral and six terminal spines arranged as follows: a median pair, an outer pair nearly twice as long as the median and above the bases of the outer pairs a third much smaller pair similar to the spinules of the dorsolateral series. Eyes large with a prominent ocellus which, however, is not completely detached from the cornea. Antennular peduncle short, the stylocerite reaching about to the end of the first segment. There is a strong spine on the antennal peduncle below the base of the scale. Antennal scale with the outer spine reaching very little beyond the narrowly truncate end of the blade. Third maxillipeds extend beyond the antennal scale by the entire length of the terminal segment which is shorter than the penultimate. All of the pereiopods are very long and slender, the last three pairs extending far beyond the tip of the rostrum. First pair extend beyond the antennal scale by the entire propodus and dactyl and half of the carpus. Second legs subequal, extending beyond the antennal scale by the chela and a little more tran half of the carpus; the latter is made up of 20 to 23 segments. Third legs extend beyond the antennal scale by the distal sixth of the merus and all of the succeeding segments; the propodus is 15 times as long as the dactyl and 1.16 times the length of the carpus. Fourth leg reaches as far forward as the third and extends beyond the antennal scale by the last two segments and four-fifths of the carpus; the propodus is 20 times as long as the dactyl and 1.7 times as long as the carpus. Last legs do not extend quite as far forward as the two preceding pairs, reaching beyond the antennal scale by the dactyl and propodus and half of the carpus; the propodus is 21 times the length of the dactyl and 1.9 times as long as the carpus.

Measurements of holotype.—Total length about 70 mm.; length of carapace 12.5 mm.; length of rostrum 23 mm.

The unarmed distal portion of the rostrum and the widely spaced ventral teeth separate this species at a glance from most of the known forms of both *Plesionika* and *Parapandalus*. It seems to show the closest affinities with *Plesionika alcocki* (Anderson), *Plesionika uniproducta* Bate and *Parapandalus cottei* (Kotte). From the first it is distinguished by the presence of an ocellus on the eyestalk and the more recurved rostrum. *Plesionika uniproducta* differs likewise in lacking an ocellus and also in having shorter pereiopods and the anterior tooth of the dorsal crest at a greater distance from the preceding teeth. *Parapandalus cottei* appears similar, but apparently has no dorsal teeth behind the margin of the orbit.

Family Glyphocrangonidae

Glyphocrangon alispina, sp. nov.

Holotype.—Ovigerous female M. C. Z. No. 10242, off Bahia Cardenas, Matanzas Province, Cuba, Lat. 23° 24′ N., Long. 81° 00′ 30″ W., 370-605 fathoms, March 16, 1938; station 2995.

Paratype.—Ovigerous female Nicholas Channel, north of Santa Clara Province, Cuba, Lat. 23° 16′ N., Long 80° 11′ W., 415 fathoms, March 14, 1938; station 2990-A.

Integument covered with a short, dense pubescence. Carapace with dorsal crests farther apart in front of the cervical groove than behind it; the portion behind the groove armed with three or four obtuse tubercles, that in front with six or seven; area between the crests smooth, without tubercles. Second crest with four tubercles behind the cervical groove; this crest becomes obscure anteriorly, being indicated by about four tubercles, the anterior being placed almost directly above the preceding one, and anterior to these a strong spine on the margin of the hepato-gastric groove. Third crest pitted but not tuberculate, the posterior portion ending in a spine with a tubercle just above and anterior to it, the anterior portion armed with a small, slender spine followed by the long, slender, remarkably outstanding antennal spine. Fourth crest pitted, unarmed, the anterior portion terminating just before reaching the slender branchiostegal spine; the latter curves upward slightly and terminates about on a level with the anterior margins of the eyes, extending slightly beyond the level of the tips of the antennal spines. Fifth crest indicated by two short, pitted elevations. Except for the crests and tubercles mentioned, the carapace is smooth beneath the pubescence. Rostrum slender, upturned at the tip, slightly longer than the carapace and smooth except for a low median dorsal carina and two pairs of spines, one at the base and another pair just behind the anterior margins of the eyes. Abdomen, including the telson, almost exactly as in *G. nobilis* A. Milne Edwards. The eggs measure about 2.8 mm. across their greatest diameter.

Measurements of holotype.—Total length 71 mm.; length of carapace 16.8 mm.; length of rostrum 17.7 mm.; distance between tips of antennal spines 18.1 mm.

This species is very similar to *G. nobilis* A. Milne Edwards from which it differs most noticeably in the very long and outstanding antennal spines which, in *G. nobilis,* are little if at all more divergent than the branchiostegal spines. The third carina of the carapace is somewhat more prominent in its posterior half in the present species so that that portion of the carapace appears broader in dorsal view. Finally, the posterior portion of the third carina terminates anteriorly in a relatively strong spine, whereas in *G. nobilis* there is merely a low right angle at the most.

Glyphocrangon (Plastocrangon) caecescens atlantica, subsp. nov.

Holotype.—Female, M.C.Z. No. 10243, south of Santa Clara Province, Cuba, Lat. 20° 47′ N., Long. 80° 24′ W., 2125 fathoms, February 26, 1938; station 2966.

This form is very near *G.* (*P.*) *caecescens* Wood-Mason from the Bay of Bengal (see: Alcock, Descr. Catal. Indian Deep-Sea Crust. Decap. Macrura and Anomala, 1901, p. 133) but it differs in the following relatively minor characters. The rostrum is armed with two pairs of spines instead of three, a single basal pair and a pair at about the level of the anterior margin of the eyes. The anterior portion of the third crest of the carapace, which is said to be lacking in the Indian form, is indicated by a row of five or six tubercles. The two teeth on the anterior portion of the fourth crest behind the branchiostegal spine are reduced to low, obtuse lobes. The abdomen is as in the typical form except that the pleura of the fifth somite is armed with but two teeth, the posterior of which is the larger, rather than bearing a dentiform angle either side of a central tooth as on the second somite.

Measurements. — Total length 94.8 mm.; length of carapace 23.2 mm.; length of rostrum 20.2 mm.

Apparently there is but one known specimen of the typical form of this species, a male which was considerably smaller than the present female. It is impossible to tell, therefore, whether the differences noted between these two specimens are constant or whether they are individual, sex or age differences. It is perhaps significant that both the Indian specimen and this one, apparently the first member of the subgenus to be recorded from the Atlantic, were taken from very deep water.

Family Homaridae

Eunephrops cadenasi, sp. nov.

Holotype.—Female, M.C.Z. No. 10235, Nicholas Channel south of Cay Sal Bank, Lat. 23° 21′ N., Long. 79° 58′ W., 300-315 fathoms, March 13, 1938; station 2987-C.

Allotype.—Male, M.C.Z. No. 10236, south end of Santaren Channel, S.E. of Cay Sal Bank, Lat. 23° 23′ N., Long. 79° 17′ W., 250 fathoms, March 12, 1938; station 2985.

Carapace about as broad as high, covered with a short pubescence placed among rather closely set low tubercles which become sharpish granules anteriorly. The very deep cervical suture which passes over the back, a second deep suture in the form of an inverted Y behind the hepatic region, a submarginal groove extending along the edge of the carapace from one hepatic region to the other and an impressed, colorless line extending along the dorsal midline from the middle of the rostrum to the posterior margin of the carapace are all quite smooth and devoid of either pubescence or tubercles. Antennal spine strong, flattener dorso-ventrally, extending from the margin of the carapace behind the base of the antenna nearly as far as the tips of the eyes. Behind this, on the middle of the hepatic region is a much smaller, sharp spine and, directly above the last and some distance behind the orbit, is a similar spine. Rostrum very similar to that in *Homarus;* it curves down in the proximal two-thirds of its length and then ascends slightly to the tip. There are two pairs of strong dorsolateral spines on the proximal portion and a single small ventral denticle on the distal third. Behind the base of the rostrum are two other spines, the anterior pair similar in size and form to the lateral rostral spines but spaced farther apart; the second pair are much smaller, scarcely as large as the hepatic and postorbital spines. There is an enlarged roughened tubercle on either side of the dorsal midline of the carapace on the posterior margin of the cervical suture, but no spines. Eyes large, reniform and black. Antennular peduncle reaching as far as the lowest point of the rostrum. The second segment of the antennal peduncle is armed with a distinct spine at the base of the scale. The latter is about three-fourths as long as the fourth segment of the peduncle, about one-half as wide as long and armed with a well-marked terminal spine. Antennular flagella of subequal length, about as long as the distance from the posterior pair of postrostral teeth to the posterior margin of the carapace. Antennal flagella nearly two and one-half times as long as the carapace and rostrum. Large chelipeds similar in form to those of *Nephrops*. Merus armed with a single large terminal spine on the dorsal margin preceded by several small spines or denticles. The ventral margin has two large spines near the distal end. Carpus armed with many spines and denticles of all sixes. Hand with two parallel rows of blunt spines on each margin and a single row along the middle of either face. Fingers about as long as the palm and crossed at the tips. Second and third legs provided with small chelae fringed with setae; the palm of the second leg is 3.32 times the length of the dactyl. Fourth and fifth legs of similar form, the dactil being of very nearly the same structure as those of the second and third legs, but there is no prolongation of the propodus to form a chela; the propodus of the fourth leg is 3.07 times the length of the dactyl. Abdomen everywhere somewhat pubescent, especially so in the interrupted transverse dorsal sulci of the second to fifth somites. The sixth segment has a few tubercles set in the pubescence and the telson likewise has two tubercular areas either side of the shallow median depression. There are a few lateral denticles on the proximal half of the telson and a spine at either distal angle.

Measurements of holotype.—Total length from tip of rostrum to tip of telson 224 mm.; length of carapace and rostrum 112 mm.; length of rostrum 32.8 mm.; length of large cheliped 202 mm.

The male allotype is only 144 mm. long, the carapace and rostrum measuring 68 mm. It differs from the type in having no ventral denticle on the rostrum, the anterior rostral spine on the left side is missing, there are two pairs of small spines behind the postrostral spines instead of one, there is only one distal ventral spine on the merus of the left cheliped (two on the right), the smooth mid-dorsal line on the carapace is distinct only on the rostrum and behind the cervical groove and the sternites of the second to fifth abdominal somites are armed with strong median spines.

The color in the preserved specimens is a salmon pink on the dorsal surface of the carapace and rostrum, fingers and distal portions of the hands of the large chelae, the dactyls and the distal portions of the propodi of the remaining legs. Except for the tips of some of the larger spines on the chelipeds which are also salmon pink, the animal elsewhere is white.

The present species appears to be superficially very like the only previously known species in the genus, *Eunephrops bairdii* Smith (Proc. U. S. Nat. Mus., vol. 8, 1885, p. 167), which is known only from the holotype female taken in the Gulf of Darien. *E. cadenasi* can be readily distinguished from the genotype, however, by the absence of spines on the posterior margin of the cervical suture near the dorsal midline of the carapace, by the presence of a distinct spine on the second segment of the antennal peduncle at the base of the antennal scale, by the form of the antennal scale which attains the distal fourth of the fourth segment of the peduncle and terminates in a well-marked tooth rather than reaching little more than halfway along the fourth segment and ending in a minute tooth as in Smith's species and by the relative length of the palm of the second chela which is three and one-third times as long as the dactyl rather than little more than twice as long and the correspondingly long propodus of the fourth leg which is more than three times as long as the dactyl rather than less than twice as long.

These differences all seem to ally this species more closely to *Homarus* than to *Nephrops*. In fact, with the exception of the large chelipeds, the entire aspect of the animal is very like that of *Homarus*.

This species is named for Dr. José M. Cadenas, Rector of the University of Havana, who deserves acclaim for aiding both in the organization and in bringing to a successful conclusion the present "Atlantis" expedition.

Family Uroptychidae

Uroptychus aguayoi, sp. nov.

Holotype.—Ovigerous female, M.C.Z. No. 10232, western part of Northwest Providence Channel, Bahamas, Lat. 26° 14′ N., Long. 78° 43′ W., 285 fathoms, February 3, 1938; station 2950.

Carapace, not including the rostrum, as long as broad at the posterior third; smooth and unarmed dorsally. It is armed laterally with a large spine at the anterolateral angle followed by a small spine then, between the anterior and posterior branches of the cervical groove, a very large spine with one or two denticles on its posterior slope. Behind the posterior branch of the cervical groove is a medium sized spine followed by six or seven denticles. Following these, the posterior fourth of the lateral margin is smoothly carinate with a submarginal gutter extending a little around the posterolateral angle of the carapace. Rostrum about twice as long as broad at base, more than twice as long as the eyestalks, slightly convex laterally and deeply channeled dorsally. Thoracic sternum with a small spine either side of the anterior emargination and a very large spine at the base of each cheliped. Third maxillipeds unarmed except for the usual pectinate inner margin of the ischium. Chelipeds three times as long as the carapace and rostrum. Merus about three-fourths as long as the carpus which, in turn, is two-thirds as long as the chela. Ischium armed with a long spine at both the upper and lower articulations with the merus and a few additional tubercles on the inner surface. Merus with from 14 to 16 long spines roughly arranged in three longitudinal rows on the inner and upper surfaces, as well as six similar spines at the articulation with the carpus. Carpus covered with numerous low denticles and armed with six spines at the distal articulation. Chela totally unarmed. Ambulatory legs with a dorsal spine on the ischium, about four dorsal denticles on the proximal half of the merus and a spine at the distal end of the lower margin of that segment. There are two to four small movable spines near the distal end of the lower margin of the propodus. Dactyls with about nine ventral teeth which increase in size distally.

Measurements. — Length of carapace and rostrum 13.3 mm.; breadth of carapace 7.9 mm.; length of rostrum 5.5 mm.; length of eyestalk 2.0 mm.; length of chelipeds 40.0 mm.

This species is similar to *U. spiniger* Benedict from off Havana, but differs in having a broader rostrum, much more spiny chelipeds and the absence of spines on the meral and carpal joints of the third maxillipeds. From *U. bellus* Faxon it is distinguished by the broader rostrum and absence of spines on the chelae and ambulatory legs. It is rather close to *U. bouvieri* Caullery but that species has more spines on the propodi of the ambulatory legs and the spines on the carpus of the chelipeds are stronger. *U. naso* van Dam has the rostrum toothed, the meri of the ambulatory legs coarsely serrate and the chelae spinulous. From all other known species *U. aguayoi* may be separated by the spinose lateral margins of the carapace and chelipeds, the absence of gastric spines and the reduction of the spines on the propodi of the ambulatory legs.

This species is named for Dr. C. G. Aguayo, Assistant Professor of Zoology at the University of Havana.

Family Galatheidae

Munida schroederi, sp. nov.

Holotype.—Male, M.C.Z. No. 10216, 8 miles N.E. of Great Isaac Island, north of the Bimini Group, Bahama Islands, Lat. 26° 08′ N., Long. 79° 02′ W., 155 fathoms, February 3, 1938; station 2951.

Paratypes.—10 males, 9 females (4 ovigerous) from the same station.

2 males, 5 females (4 ovigerous), Bahia de Cochinos, Santa Clara Province, Cuba, Lat. 22° 07′ N., Long. 81° 08′ 30″ W., 270 fathoms, February 18, 1938; station 2960.

9 males, 8 females (4 ovigerous), Bahia de Cochinos, Lat. 22° 07′ N., Long. 81° 08′ W., 190-210 fathoms, February 23, 1938; station 2961-C.

11 males, 12 females (10 ovigerous), Bahia de Cochinos, Lat. 22° 07′ N., Long. 81° 08′ W., 195-235 fathoms, February 23, 1938; station 2961-D.

6 males, 3 ovigerous females, Bahia de Cochinos, Lat. 22° 07′ N., Long. 81° 08′ W., 200-210 fathoms, February 24, 1938; station 2962.

4 males, 2 ovigerous females, Bahia de Cochinos, Lat. 22° 07′ N., Long. 81° 08′ W., 180-190 fathoms, February 24, 1938; station 2962-B.

6 males, 7 females (5 ovigerous), Bahia de Cochinos, Lat. 22° 07′ N., Long. 81° 08′ W., 210 fathoms, February 24, 1938; station 2962-C.

2 ovigerous females, Bahia de Cochinos, Lat. 22° 07′ N., Long. 81° 08′ W., 175-210 fathoms, February 24, 1938; station 2962-D.

56 males, 74 females (69 ovigerous), Bahia de Cochinos, Lat. 22° 07′ N., Long. 81° 08′ W., 190-180 fathoms, February 25, 1938; station 2963.

3 males, 5 females (4 ovigerous), Bahia de Cochinos, Lat. 22° 07′ N., Long. 81° 08′ W., 205 fathoms, February 25, 1938; station 2963-C.

2 ovigerous females, entrance to Bahia Matanzas, Matanzas Province, Cuba, Lat. 23° 10′ N., Long. 81° 29′ W., 170-255 fathoms, March 21, 1938; station 3000.

6 males, 6 females, north coast of Cuba; station ?

Carapace broad, depressed and very spinose. It is widest at the posterior third. Rostrum more than twice as long as the supraocular spines which reach only to the middle of the eyes. Gastric spines behind and slightly outside of the line of the supraoculars. A pair of spines directly behind the gastric. There may be a single median spine between the supraocular and gastric spines. There is a large spine followed by a smaller one on the midline of the gastric region and three prominent median spines on the cardiac region. The remainder of the carapace is covered with many spines arising from the transverse striae, the most prominent of which form a longitudinal row of three to five on the inner branchial region either side of the anterior cardiac region. There are six lateral spines behind the postantennal spine. The posterior margin bears about twelve small spines. Second and third abdominal somites armed with four widely spaced spines on the anterior margin and one, somites two, pairs of smaller ones near the posterior margin. The fourth somite is similarly armed with four anterior spines, but near the posterior margin are three or five closely set spines, one of which is median. Third maxillipeds armed with a long spine at the anterolateral angle of the ischium and a similar spine at the middle of the inner margin of the merus. The chelipeds are a little less than four times the length of the carapace and rostrum. Merus subquadrate with rows of spines at each angle except the outer ventral. Carpus somewhat more cylindrical due to the absence of the row of spines on the outer dorsal angle and the reduction of those on the inner ventral angle to a single spine. Palm also subcylindrical with a row of spines at the internal dorsal angle and two or three scattered ones on the external face. Fingers slightly shorter than the palm; the fixed finger curves outward at the base to form a slight gape in the male and terminates in a fork. Ambulatory legs flattened. The meri have a row of spines on either margin, the carpus a dorsal or anterior row and a single subterminal spine on the ventral or posterior edge, the propodus is unarmed except for a single small subterminal spine on the posterior margin. The dactyls are sinuous with a proximal lobe on the lower margin, and unarmed.

Measurements of holotype.—Length from tip of rostrum to end of telson 32.8 mm.; length of carapace and rostrum 15.8 mm.; greatest breadth of carapace 11.8 mm.; length of rostral spine 3.8 mm.; length of cheliped 60.3 mm.

M. schroederi is apparently closely related to *M. hispida* Benedict from American Pacific waters. Although the carapace is hispid and similar in form, the Atlantic species is easily distinguished by the shorter rostral and much shorter supraocular spines, the gastric spines are placed much farther apart and there is but one, rather than two, spines on the inner margin of the merus of the third maxillipeds.

This species is named for Mr. William C. Schroeder, leader of the expedition.

Munidopsis bermudezi, sp. nov.

Holotype.—Ovigerous female, M.C.Z. No. 10231, S.E. of Bahia de Guantanamo, Oriente Province, Cuba, Lat. 19° 43′ 30″ N., Long. 74° 57′ 30″ W., 1330-1650 fathoms, March 4, 1938; station 2967-B.

Paratype.—One female, north of Gibara, Oriente Province, Cuba, Lat. 21° 19′ N., Long. 76° 05′ W., 1450 fathoms, March 8, 1938; station 2976.

Carapace scarcely longer than broad, everywhere densely pubescent except for a bare spot either side of the anterior boundary of the cardiac region and another pair lateral to the postgastric region. There is a strong postantennal tooth, another at the anterolateral angle separated from the first by a nearly semicircular emargination; immediately behind the anterolateral tooth is a third of nearly the same size followed by four or five denticles diminishing in size posteriorly. Behind the posterior branch of the cervical groove the carapace broadens abruptly, forming a prominent tooth; the carapace is broadest at this point. Behing this tooth the lateral margin is armed with two or three denticles and several prominent rugae. The only armature on the dorsal surface of the carapace is a pair of prominent postrostral spines on the gastric region. Under the pubescence the carapace is largely smooth except for a few low tubercles and scattered short rugae on the posterior third. Rostrum simply triangular, much less than half the length of the remainder of the carapace and bluntly carinate in the dorsal midline. Abdomen densely pubescent like the carapace. Second, third and fourth somites bicarinate dorsally, the anterior carina of each somite extending nearly to the margin of the pleura, the posterior confined to the terga. Last three somites largely smooth and punctate beneath the pubescence. Eyestalks immovable and armed with a strong distal spine at the base of which is set obliquely the minute, colorless cornea. Merus of the third maxillipeds armed on the internal margin with three sharp teeth. All of the legs are covered dorsally with long hair. Chelipeds shorter than the carapace plus the rostrum, armed with a spine on the ischium, a row of six strong spines on the dorsal angle of the merus as well as two other spines at the distal end of that joint, five similar spines on the carpus and a single smaller spine on the margin of the hand near the base of the dactyl. The hand is very short and broad with the fingers about the same length as the palm. First ambulatory legs with a spine on the ischium, a row of six spines on the merus, six on the carpus and two on the propodus. Second legs with an ischial spine, six or seven on the merus, four or five on the carpus and possibly two, sometimes none, on the propodus. Third legs with no ischial spine, four on the merus, four or five on the carpus and none or possibly one on the propodus. Dactyls of all three legs armed on the ventral border with six or seven small spines. The holotype carries about 75 round, colorless eggs, about 2.5 mm. in diameter.

Measurements of holotype.—Total length about 69 mm.; length of carapace plus rostrum 37.7 mm.; breadth of carapace 27.0 mm.; length of rostrum 10.2 mm.

This species is distinguishable from all other robust species of *Munidopsis* by the combination of a single pair of gastric spines, immovable eyestalks, large single ocular spine and very reduced cornea. It closely resembles the figure of *M. ceratophthalmus* Alcock (Catal. Indian Deep-Sea Crust. in Indian Mus., 1901, p. 271, pl. 3, fig. 2). The eyes are of the same form as in that species, but the lateral spine behind the posterior branch of the cervical groove is much larger in the ''Atlantis'' specimens and there are two spines on the gastric region which are absent in Alcock's species.

This species is named for Dr. P. J. Bermudez of the University of Havana, a member of the expedition.

Munidopsis riveroi, sp. nov.

Holotype.—Male, M.C.Z. No. 10230, Nicholas Channel north of Santa Clara Province, Cuba, Lat. 23° 10′ N., Long. 80° 04′ W., 360 fathoms, March 14, 1938; station 2989.

Paratype.—Ovigerous female from the same station.

Carapace without spines, well areolated, the highest points being on the gastric and cardiac regions. The raised portions are coarsely tuberculate, the depressed areas smooth and pubescent. Rostrum two-thirds as broad as long and partially covering the eyes. It is deeply hollowed dorsally by a broad longitudinal furrow, abruptly narrowed beyond the eyes and then drawn out to a minutely denticulate point so that the distal margins are sinuous. Apex slightly upturned so that the rostrum appears sinuous in lateral view. Second, third and fourth abdominal segments transversely bicarinate with a low median tooth on each carina. Eyes movable, comparatively large, unpigmented and unarmed. Merus of third maxillipeds with two teeth near the middle of the inner margin. Chelipeds about two and one-half times as long as the carapace plus the rostrum. Palm longer than the fingers. All of the joints are scabrous and the merus is armed on the inner margin with three evenly spaced, conical spines. Merus and carpus of ambulatory legs without spines, scabrous, the merus distinctly carinate dorsally. Propodus smooth and pubescent. Dactyl curved and armed on the lower margin with four strong teeth which increase in size distally.

Measurements of holotype.—Total length from tip of rostrum to end of uropods 36.3 mm.; length or carapace plus rostrum 17.8 mm.; breadth of carapace 11.7 mm.; length of rostrum 5.0 mm.; length of cheliped 46.2 mm.

The peculiar form of the rostrum and the totally unarmed carapace readily distinguish this species from all previously described.

This species is named for Dr. Luis Howell Rivero of the University of Havana, who was a member of the expedition.

Family Paguridae

Pylopagurus cavimanus, sp. nov.

Holotype.—Female, M.C.Z. No. 10233, Bahia de Cochinos, Santa Clara Province, Cuba, Lat. 22° 07′ N., Long. 81° 08′ W., 150-170 fathoms, February 25, 1938; station 2963-B.

Median projection of front obtuse, more prominent than the rounded lateral projections and terminating in a minute acute tooth; lateral projections also armed with a minute laterally directed tooth. Eyestalks slender, nearly three-fourths as long as the anterior part of the carapace with prominent styliform lateral scales. Antennal scale hairy, styliform, reaching to the middle of the terminal segment of the antennal peduncle and about to the distal fourth of the eyestalks. Right cheliped with a row of short spines on the lower margin of the merus and a number of strong spines scattered over the upper surface of the carpus. Chela very narrow proximally where it slightly overhangs the carpal articulation, twice as long as broad, slightly convex dorsally in a longitudinal direction and so strongly concave transversaly that the lateral margins are very nearly perpendicular. The margins are everywhere armed with spines of irregular length and the dorsal surface is paved with low, roughly circular tubercles. The fingers are similarly ornamented with marginal spines and low tubercles. The left or smaller cheliped has a row of strong spines on the outer edge of the dorsal surface of the carpus and a similar row extends along the outer margin of the palm and fixed finger. The outer half of the upper surface of the chela has a few scattered spines, the inner half is smooth and sparsely hairy. First two pairs of ambulatory legs unarmed except for the dactyl which bears 20-25 spine-like setae on the dorsal edge and nine short spines on the ventral margin. Propodus of the fourth legs produced ventrally nearly to the middle of the dactyl and armed on the lower edge with several rows of short spines. Dactyl with a row of short spines on the distal two-thirds of the ventral margins. Propodus and dactyl of the last legs with densely spinose areas dorsally.

This species is at once distinguished from all other species of the genus by the extremely concave, trough-like larger chela.

Family Lithodidae

Paralomis cubensis, sp. nov.

Holotype.—Female, M.C.Z. No. 10234, east of Havana, Cuba, Lat. 23° 12′ 30″ N., Long. 82° 12′ W., 240-300 fathoms, March 22, 1938; station 3003.

Paratype.—Female with a large rhizocephalid from the same locality.

Carapace not including the rostrum about as long as broad, covered with crowded tubercles of different sizes; on most of the dorsal surface these tubercles are low and rounded, but they become more and more acute toward the margins. There is a smooth, wartlike prominence either side of the gastric region in the cervical groove. There is no distinct spine on the gastric region although several of the anterior tubercles are acute. Margin of hepatic region armed with about six strong spines of different sizes, including the outer orbital spine. Behind the cervical groove the lateral margin of the branchial region is armed with a row of four or five spines followed by ten to twelve progressively smaller spines reaching around the posterolateral margin to about the median third of the posterior margin. The sulci either side of the cardiac region converge posteriorly but do not meet. Orbits rather deeply excavate. Rostrum trispinose, the dorsal pair of spines smaller than the inferior and the latter unarmed below; there is a pair of smaller spines at the base of the rostrum and a very small spine of sharp tubercle just anterior to this pair. Eyestalks constricted in the middle and armed with several small spines or sharp granules, the largest being terminal and extending well beyond the cornea. Antennal peduncle with a small outer spine on the first segment and a long spine with a second smaller spine at its base on the second segment. Acicle with from four to six spines, the strongest being a terminal pair forming a fork, one on the dorsomedian surface behind the inner spine of the terminal pair and a fourth still more proximad on the outer margin. Chelipeds subequal in length but the right is much more robust than the left; all of the segments are strongly spinose. Ambulatory legs compressed, most markedly so on the first pair. Meri of the first two pairs armed with two rows of dorsal spines and a few sharp denticles scattered over the lateral surface. Merus of the third ambulatory legs with several strong spines on the lateral surface in addition to the two dorsal rows. Carpus and propodus of all of the legs very spiny. Dactyl with five strong dorsal and lateral spines near the base and eight to twelve slender, dark, corneous ventral spines in addition to the long, dark terminal spine. Second segment of the abdomen entire and covered, like the carapace, with setiferous tubercles which become blunt spines laterally. Third to seventh segments with a few very low scattered tubercles bearing long setae. Central portion of the sixth somite very little longer than that of the fifth. Outer margins of the left lateral portions of the third to fifth segments evenly convex and coarsely crenulate or spinose.

Measurements of holotype. — Length of carapace and rostrum 61.2 mm.; length of rostrum 8.0 mm.; greatest breadth of carapace, not including spines 53.0 mm.; length of larger schela 80.8 mm.; length of second ambulatory leg 100.0 mm.

Paralomis cubensis is apparently the first member of the genus to be recorded from the tropical Atlantic. It can be distinguished from most of the described species by the absence of spines on the gastric region, the strong lateral spines of the carapace, the failure of the lateral cardiac furrows to meet posteriorly, the absence of a central tooth on the median rostral spine and the moderately compressed ambulatory legs. The present species seems to show the nearest relationship to *P. investigatoris* Alcock and Anderson which, however, has three large outer spines and three small inner spines on the acicle of the antennal peduncle, and to *P. verrilli* (Benedict) which is distinguished by the more expanded branchial regions, a single gastric spine, the cardiac region closed posteriorly and shorter anterolateral spines.

Family Calappidae

Paracyclois atlantis, sp. nov.

Holotype.—Female, M.C.Z. No. 10212, Old Bahama Channel due north of Punta Alegre, Camaguey Province, Cuba, Lat. 22° 45′ N., Long. 78° 45′ W., 150-180 fathoms, March 11, 1938; station 2982-E.

Carapace everywhere finely granular and coarsely punctate, distinctly wider than long. Posterolateral margin with four large and one or two rudimentary spines. Posterior margin trilobate and coarsely granular but not toothed. Front deflexed to a vertical plane anteriorly, broadly triangular; inner orbital angles not reaching nearly as far as the tip of the front. Second abdominal somite strongly trilobate; the sixth somite 1.4 times as broad as long, constricted at the distal third. Third maxillipeds coarsely granular, the ischium provided with a deep but narrow notch at the insertion of the palp. Subdistal crest of merus of chelipeds subparallel to distal margin and armed with four or five denticulate spines. Upper margin of hand set with seven low, closely set teeth. Lower margins of meri of all ambulatory legs spinose.

Measurement.—Length of carapace 45.5 mm.; breadth of carapace 49.1 mm.

The greater proportionate breadth of the carapace, lack of teeth on the posterior margin, form of the front, narrower notch on the merus of the third maxillipeds, position and denticulate form of the teeth of the subdistal crest on the merus of the chelipeds and the presence of ventral spines on the meri of all of the ambulatory legs serve to distinguish this species from *P. milne-edwardsii* Miers from off the Admiralty Islands. The completely deflexed front and smaller posterolateral spines on the carapace separate it from the subfossil *P. grandispinis* Etheridge and McCulloch from Melbourne, Australia.

Family Xanthidae

Tetraxanthus rathbunae, sp. nov.

Tetraxanthus bidentatus Rathbun, Bull. Labor. Nat. Hist. State Univ. Iowa, vol. 4, 1898, p. 275; Bull. U. S. Nat. Mus., vol. 152, 1930, p. 458, pl. 184. Not *Xanthodes bidentatus* A. Milne Edwards, Crust. Reg. Mexico, 1880, p. 353, pl. 53, figs. 5-5b.

Holotype.—Male, M.C.Z. No. 10213, Old Bahama Channel due north of Punta Caldera, Camaguey Province, Cuba, Lat. 22° 44′ 30″ N., Long. 78° 41′ W., 150-180 fathoms, March 11, 1938; station 2982-D.

Paratypes.—One male, one ovigerous female, Old Bahama Channel due north of Punta Alegre, Camaguey Province, Cuba, Lat. 22° 45′ N., Long. 78° 45′ W., 150-180 fathoms, March 11, 1938; station 2982-E.

One male, western end of Old Bahama Channel off north coast of Cuba, Lat. 23° 11′ N., Long. 79° 08′ W., 235-260 fathoms, March 12, 1938; station 2983.

Thanks to a query made by Mr. John S. Garth, the holotype of *Xanthodes bidentatus* A. Milne Edwards collected by the ''Blake'' off Grenada was found to be quite distinct from this species. The ''Blake'' specimen is apparently identical with *Tetraxanthus rugosus* Rathbun, 1930, which therefore must be synonymized.

T. rathbunae differs from *T. bidentatus* in its more convex carapace and less prominent anterolateral teeth. The front is not so distinctly bilobate nor is it sharply marked off from the internal angles of the orbit as in the ''Blake'' species. The carpus and hand of the chelipeds are smooth with a single lobe on the inner margin of the carpus, whereas in *P. bidentatus* the carpus and proximal portion of the outer surface of the palm are distinctly rugose and there is a second smaller tooth below and behind the prominent inner carpal tooth.

Family Chloridellidae

Chloridella heptacantha, sp. nov.

Holotype.—Male, M.C.Z. No. 10245, Bahia de Cochinos, Santa Clara Province, Cuba, Lat. 22° 07′ N., Long. 81° 08′ W., 180-190 fathoms, February 24, 1938; station 2962-B.

Paratype.—Male, Old Bahama Channel due north of Punta Alegre, Camaguey Province, Cuba, Lat. 22° 45′ N., Long. 78° 45′ W., 150-180 fathoms, March 11, 1938; station 2982-E.

Carapace armed with long spines at the anterolateral angles which do not, however, reach as far as the base of the rostrum. Posterolateral margin angular. Both parts of the median dorsal carina, the main anterior portion and the short carina behind the cervical groove, are bifurcate anteriorly. The marginal carinae are distinct, extending from the anterolateral spines nearly to the median third of the posterior margin of the carapace where they recurve onto the dorsal surface; lateral carinae sharp and entire, reaching from the anterolateral spines almost to the posterior margin of the carapace; intermediate carinae distinct anteriorly where they extend nearly to the anterior margin of the carapace. Rostrum longer than broad at base, noticeably narrowed anteriorly and provided with median and marginal carinae. The free thoracic somites each bear submedian and intermediate carinae. The first free somite is armed with a single flattened lateral spine, which curves slightly forward, and a nearly vertical ventral spine. Second free somite with two lateral processes, the anterior either rounded or acute and directed outward and slightly forward, the posterior acute and directed outward and backward. On the third free somite, the anterior process is indicated by a small lobe at the base of the large, acute, posteriorly directed spine. Abdomen with eight distinct carinae on the first five somites and six on the sixth. The submedian carinae terminate posteriorly in spines on the fifth and sixth somites, the intermediate on all somites but the first where they end in a right angle, and the lateral on all somites. The sixth somite is armed with six spines on the posterior margin, one on each carina. Telson just as long as its greatest breadth. The median carina is feebly notched anteriorly and terminates in a strong spine. Either side of the median carina are radiating rows of obscure pits. The pre-lateral lobe is distinct but not dentate. The submedian teeth are recurved dorsally and each bears a prominent projecting lobe on its median margin. The denticles include four to seven submedian, ten to twelve intermediate and one lateral. Neither the carinae nor the margins of the telson in the male are noticeably swollen. The inferior surface is smooth either side of the post-anal carina. Uropod with a strong dorsal spine on the first segment at the articulation with the exopod. The inner spine of the ventral bifurcate process is about twice as long as the outer with a well-developed lobe on the external margin; internally this process is provided with 15 to 20 low marginal tubercles. Eye broad, the corneal axis greater than the peduncular axis, and the cornea set obliquely on the stalk. Mandibular palp present. Raptorial claw with the carpus irregularly ridged and nodose, the dorsal carina being rather low and not prominent; margin of propodus finely and evenly pectinate with three long movable proximal spines, of which the median is the smallest; dactyl armed with seven spines including the terminal one. There are epipods on the first four thoracic appendages.

Measurements of holotype.—Total length 57.8 mm.; length of carapace 13.5 mm.; greatest breadth of carapace 10.0 mm.; length of rostrum 2.0 mm.; breadth of rostrum at base 1.8 mm.; length of telson including spines 11.1 mm.; greatest breadth of telson 11.1 mm.; corneal axis of eye 3.0 mm.; peduncular axis of eye 2.5 mm.; length of antennal scale 7.9 mm.

The paratype is much smaller, being only 37.7 mm. long.

This species is apparently distinguished from all previously described forms by the combination of the following characters; seven spines on the dactyl of the raptorial claw, single spine on the first exposed thoracic somite and two projections on the second, absence of swelling on the carinae of the telson in the male and the prominent lobes on the median margins of the submedian spines of the telson.

Contribution No. 201

Reprinted from Publication No. 10 of The American Association for the Advancement of Science, pages 27–38.

THE UTILIZATION OF SOLAR ENERGY BY AQUATIC ORGANISMS

By GEORGE L. CLARKE

BIOLOGICAL LABORATORIES, HARVARD UNIVERSITY, CAMBRIDGE, MASS., AND WOODS HOLE OCEANOGRAPHIC INSTITUTION, WOODS HOLE, MASS.*

My first object in this paper is to present a brief summary of our present knowledge of the availability of radiant energy in natural waters and the utilization of it by aquatic animals and plants. My more important desire in bringing together this material, however, is to delineate the critical problems which have now arisen on this subject and upon the solution of which further significant progress depends. Research in this field falls roughly into two parts, namely, (1) the determination of the amount and nature of the light actually present at various depths in all types of water bodies, and (2) the measurement of the extent to which submerged organisms are able to utilize the light present. From the biological point of view we need to know not only the range of light intensity at any point but also its spectral composition, its angular distribution, and its distribution in time.

The solar energy which falls upon a body of water is subject first of all to a "surface loss" which in the case of the ocean may amount to as much as 60 per cent in rough weather. Only about 3 to 9 per cent of this is ordinarily due to reflection (for solar altitudes greater than 30°) and the remainder has been found to be caused by a greatly increased rate of extinction in the uppermost meter of water (Powell and Clarke 1936). It was originally suggested that this effect was due to bubbles existing near the surface but this explanation has been questioned by Poole (1938). Whether a similar increase in extinction coefficient of the subsurface stratum occurs in lakes at times when waves exist is a question which invites investigation.

As the light passes from the surface downward into the water, it is reduced in intensity according to the following equation:

$$\frac{I}{I_0} = e^{-kL}$$

where I_0 is the initial intensity, I is the final intensity, k is the extinction coefficient, L is the thickness of the layer in meters,† and e is 2.7. When this relationship between the reduction in the light and the thickness of water through which it has passed is expressed graphically on a semilogarithmic plot, a straight line is obtained (Fig. 1). The slope of the line is determined by the value of the extinction coefficient, k, which is thus an index of transparency. The extinction coefficient varies widely in the different parts of the spectrum—even for pure water—and its actual value depends upon the precise wavelength considered. In Fig. 1 the rate of absorption of red light by distilled water is seen to be very high, that for yellow light lower, and that for blue light very much lower. For example, after traversing 70 meters of distilled water blue light has suffered only a slight reduction to 70 per cent of its initial value, whereas yellow light has been reduced to 6 per cent. In the case of red light a reduction to 6 per cent has already taken place after passing through less than 3 meters of water.

Now the energy of the sun as it reaches the surface of a natural body of water is not equal in all parts of the spectrum but is distributed as shown by the uppermost curve in Fig. 2. We therefore start with

---

* Contribution No. 201.

† This quantity may be taken as the depth, but if the mean path of the light departs from the vertical, as is usually the case in natural waters, a small correction is required since the path length is then greater than the vertical depth (*cf.* Whitney 1939).

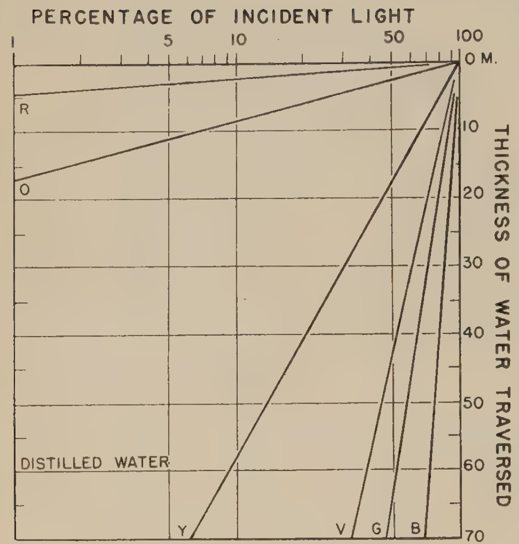


Fig. 1. Transmission of light by distilled water at 6 wave lengths within the visible spectrum. Curves show the percentage of incident light (logarithmic scale) which would remain after passing through the indicated thickness of water.

Color	Wave length[1]	Absorption per meter[2]	Extinction coefficient[3]
	Å	per cent	
Red	7200	64.5	1.1
Orange ...	6200	23.5	0.27
Yellow	5600	3.9	0.040
Green	5100	1.1	0.011
Blue	4600	0.52	0.0052
Violet	3900	1.63	0.016

[1] Mean wave length of range for each color as employed by Birge and Juday (1931).

[2] As determined for the designated wave length by James and Birge (1938).

[3] Extinction coefficient = k in the equation $I/I_0 = e^{-kL}$ where the light is reduced from I_0 to I by a stratum L meters thick. e = 2.7.

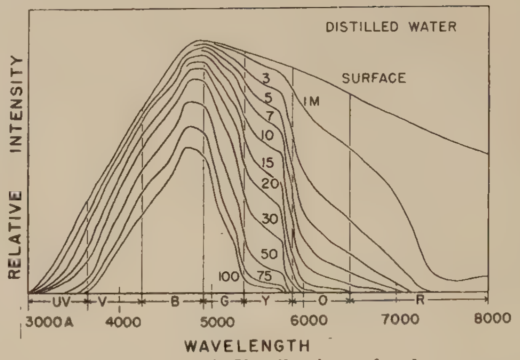


Fig. 2. The spectral distribution of solar energy at the earth's surface is given by the uppermost curve. When sunlight is passed through successive meters of pure (distilled) water, the reduction of intensity and the change in spectral distribution which result are indicated by the curves beneath (from Birge and James 1939).

unequal quantities of energy at the different wavelengths and these are absorbed at unequal rates as the light penetrates into the water. The result is that after passing through successive meters of water the spectral composition of the light present becomes rapidly and profoundly altered. The infrared and red components are reduced to small quantities within a very few meters and the ultraviolet, which was initially of small magnitude, soon drops to a minute fraction of the whole. As a consequence, after sunlight had traversed 100 meters of distilled water nothing but the blue component with a little green and violet would remain, as is demonstrated by the family of curves in Fig. 2. These curves represent the uppermost limit possible for the transparency of any body of water.

In most natural waters the rate at which light penetrates is further decreased by the presence of varying amounts of suspended particles and dissolved material. The great diversity which results in the transparency of natural waters may be appreciated by comparing the curves of light penetration for certain typical lakes and oceanic areas in various parts of the world (Fig. 3). As will appear presently, only those measurements can be fairly compared which were made within the same part of the spectrum. In the figure observations with photometers sensitive to the yellow-green region (maximum 5500Å) are presented. Sargasso water is seen to be nearly as transparent as distilled water in this spectral region and light is reduced to 1 per cent of its surface value at about 100 meters. Beyond the edge of the continental shelf 100 miles or more from the coast in both the Atlantic and the Pacific the transparency is such that the 1 per cent value is reached at about 50 meters. In coastal waters the same value occurs at between 30 and 15 meters. Although there are a few inland lakes which are as clear as typical coastal waters, the majority of them are more turbid.* In Midge Lake, for example, the illumination has been reduced to 1 per cent of its surface value at 3 meters. The extreme range of possible transparency in natural waters is thus very great.

In the various natural waters we find that the *relative* rates of absorption of *different parts of the spectrum* are not the same as those characterizing distilled water. This situation is brought about by the fact that both the suspended and the dissolved

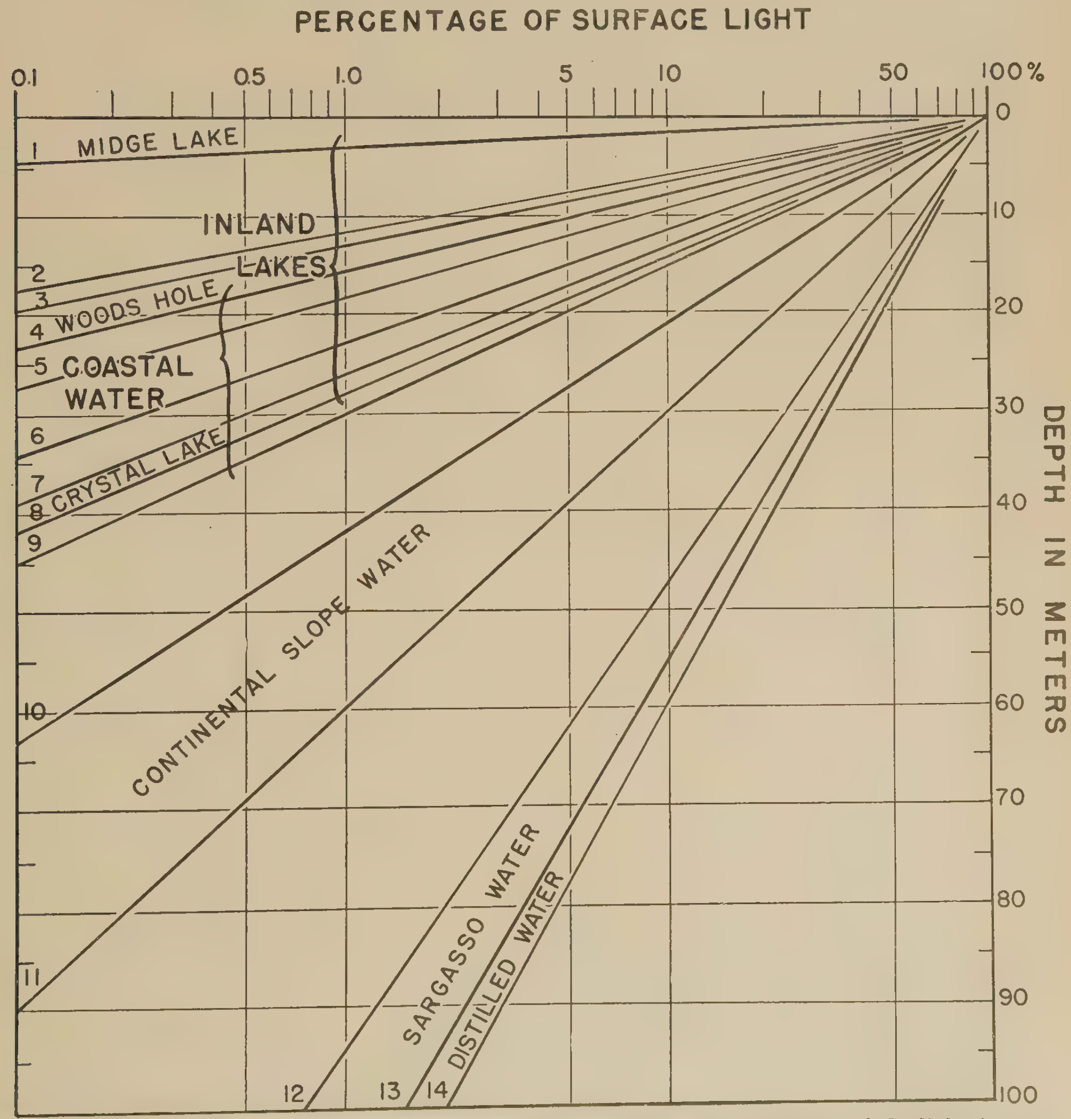


FIG. 3. Comparison of the rates of penetration of the yellow-green component of daylight into natural waters (Photometer sensitive to wave lengths 5000–6000Å). Curves show the relation between depth and illumination expressed as a percentage of the light at the surface. The curves represent the *average* value of the extinction coefficient for each series and no "surface loss" is included.

---

* A recent measurement in Crater Lake, Oregon, (Hasler 1938) yielded a depth of 40 meters for the visibility of the Secchi disc. The clearest lake which had been investigated previous to this observation was Crystal Lake, Wisconsin, in which the Secchi disc was found to disappear at about 15 meters. The transparency of Crater Lake, therefore, greatly exceeds that of any other lake in which measurements have been made.

Curve	Location	Extinction coefficient (k)	Absorption per meter %	Authority
1	Midge Lake, Wisconsin	1.53	78	Birge and Juday (1930) Fig. 15
2	Trout Lake, Wisconsin	.40	33	" " " " Fig. 14
3	Gunflint Lake, Minnesota	.36	30	Erikson (1933) at 5450Å
4	Woods Hole Harbor	.30	26	Oster and Clarke (1935) Ser. 316
5	Thatcher Pass, San Juan Islands	.256	23	Utterback and Jorgenson (1934) at 5300Å
	Buzzards Bay	.25	22	Oster and Clarke (1935) Ser. 325
6	Vineyard Sound	.20	18	" " " " Ser. 322
7	Baltic Sea	.18	16	Pettersson and Landberg (1934) Fig. 2
8	Crystal Lake, Wisconsin	.16	15	Birge and Juday (1930) Fig. 14
9	English Channel	.155	14	Atkins and Poole (1933) Ser. 58
10	Gulf of Maine (deep basin)	.11	10	Oster and Clarke (1935) Ser. 301
11	Off Vancouver Island	.079	7.6	Utterback and Jorgenson (1934) at 5300Å
	Continental Slope, s. of Nantucket Shoals	.074	7.2	Oster and Clarke (1935) Ser. 314
12	Gulf Stream	.049	5.0	" " " " Ser. 311
13	Cayman Sea (Caribbean)	.042	4.1	Clarke (1938b) Ser. 438
14	Distilled water	.039	3.8	James and Birge (1938) at 5460Å

material present have a *selective* action on light beyond that of the water itself, and the nature of the selective effect varies widely from one body of water to another. As a result it becomes necessary to measure separately the rate of penetration of each spectral region for each lake or oceanic area. Four typical cases are presented to illustrate the very great differences which are encountered in the selective action of natural waters.

In the Sargasso Sea (Fig. 4) the red part of the spectrum is absorbed at the most rapid rate, the yellow-green and violet components are reduced much more slowly, and the blue light penetrates the most effectively. The theoretical maximum for the transparency of any natural water is indicated in the figure by the distilled water curves for (1) the wavelength at which absorption is least (4730Å, k = 0.005) and (2) for the average of a band extending 500Å each side of this (av. k = 0.010). Sea water as transparent as the latter has actually been observed for limited strata in the Sargasso Sea (Clarke 1933). In Vineyard Sound (Fig. 5) the red component of sunlight is similarly absorbed more rapidly than any other, but here the yellow-green component is by far the most penetrating, and the blue and violet regions take an intermediate position. The same situation obtains in the clearest lakes as, for example, in Crystal Lake. In Trout Lake, however, although the yellow-green component still penetrates the most effectively, blue light is absorbed a little more rapidly than the red (Fig. 5). In the case of a highly colored lake like Midge Lake the relative rates of absorption are just the reverse of those in very clear water, for here we find that red light is the most penetrating and blue the least with yellow in an intermediate position (Fig. 6).

The changes in the distribution of the solar energy at increasing depths which result from the differences in the selective action of the foregoing types of water are very pronounced. The situation in the Sargasso Sea is qualitatively similar to that which would occur in distilled water (Fig. 2). The energy distribution at various levels in Crystal Lake will serve as an example for the clearest inland waters or for most coastal waters (Fig. 7). Rudolph Lake has been taken as an illustration of a highly colored lake (Fig. 8). One observes that whereas in the clearest water blue light remains after the other parts of the spectrum have been removed, in the case of Crystal Lake the energy present at 15 meters consists almost entirely of yellow and green light, and in Rudolph Lake at 5 meters the energy is practically confined to the red and orange regions.

In the foregoing cases it has been

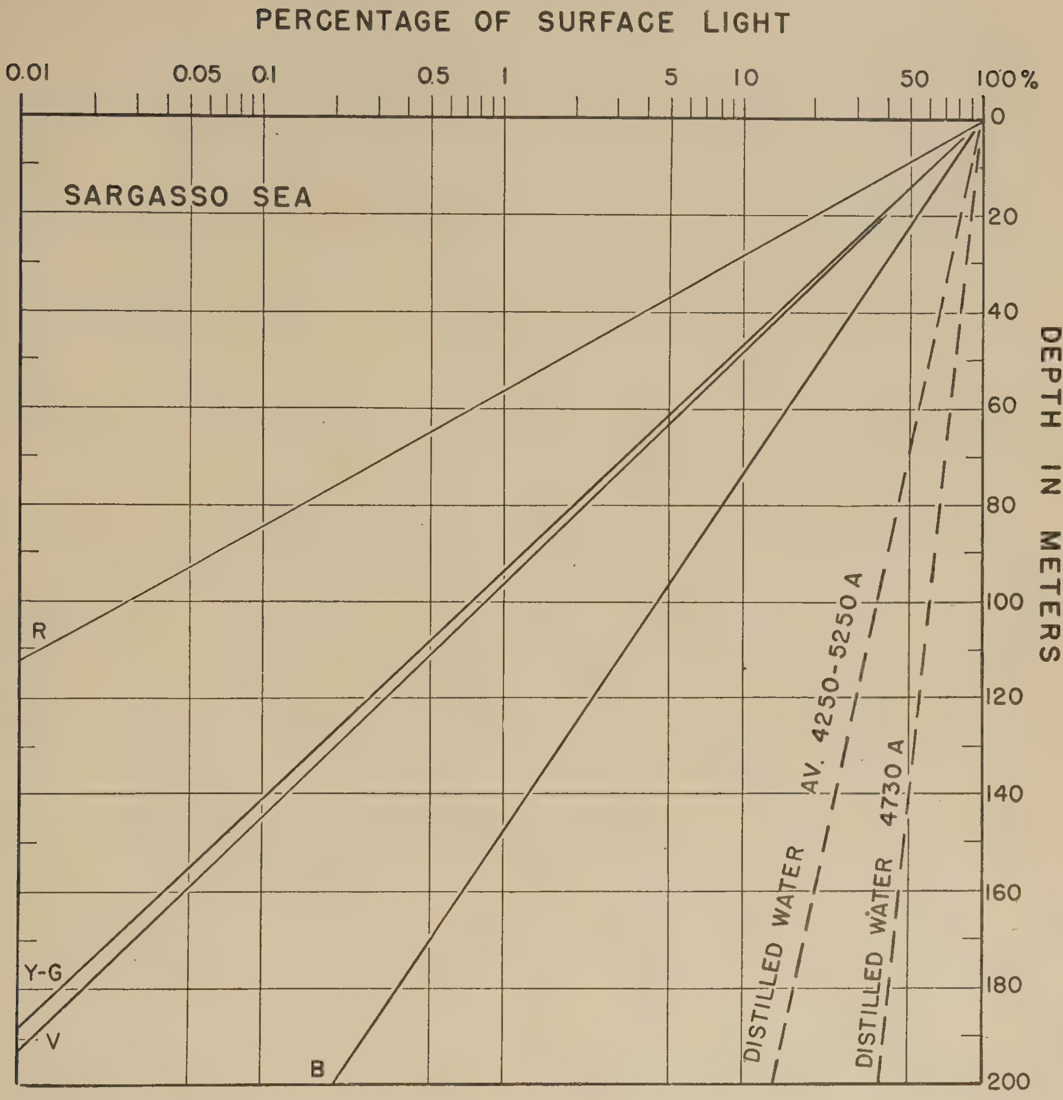


Fig. 4. Comparison of rates of penetration of four regions of the spectrum into the water of the Gulf Stream and Sargasso Sea. The curves represent the *average* values of the extinction coefficient as measured by Oster and Clarke (1935) and by Clarke (1933). The rate of penetration into distilled water for light at the wave length where absorption is least (4730Å, k = 0.005) and for light extending 500Å each side of this (av. k = 0.010) (from the data of James and Birge 1938).

assumed that the transparency of the water is uniform at all depths. This has often been found to be true especially where the water has been rendered quite homogeneous through effective mixing. In certain fjords and lakes, however, abrupt changes in transparency with depth have been reported (Pettersson 1934, Whitney 1938a). These indicate discrete layers of suspended material which may be of either organic or inorganic origin, and which may have an important function as a "false bottom." The exact identification of the material constituting such strata presents an inviting problem.

The angular distribution of the light becomes altered after it enters the water not only because of refraction at the surface but also because of scattering within the water mass. The upward component was found to be about 5 per cent of the downward component in coastal waters and about 2.5 per cent in the deep basin of the Gulf of Maine (Clarke 1936a). In the case of 16 Wisconsin lakes investigated by Whitney (1938b) this ratio ranged from 0.5 per cent to 4.8 per cent according to the lake. Within each lake, however, the light passing upwards remained a constant percentage of the downward light at all depths and the same is probably true of all oceanic areas. This finding agrees with the theoretical calculations of Whitney and is of great significance biologically because it means that the directional character of the light is not lost. Furthermore, since planktonic organisms can receive light from any direction we should have information not only on the amount of light passing vertically downward or upward but also on the radiation traversing the water at other angles. An attack on this problem has been begun by Pettersson (1938), who has found that the total light from all directions reaching a point 5 to 10 meters below the surface was 1.5 times the illumination which would have been recorded by an ordinary plane horizontal photometer. However, a great deal more work is needed on this subject (cf. Johnson and Liljequist 1938).

The distribution in time of the illumination at any point is controlled by changes in the length of day and by seasonal variation in transparency. The latter is of vital importance since it has been shown to be chiefly responsible for the tremendous differences in amount of light received daily by organisms at only moderate depths—as much as 10,000 × at 30 meters (Clarke 1938, 1939). The agents causing changes in transparency, however, are not adequately known and present another opportunity for research.

In dealing with the utilization of the light energy by aquatic animals and plants,

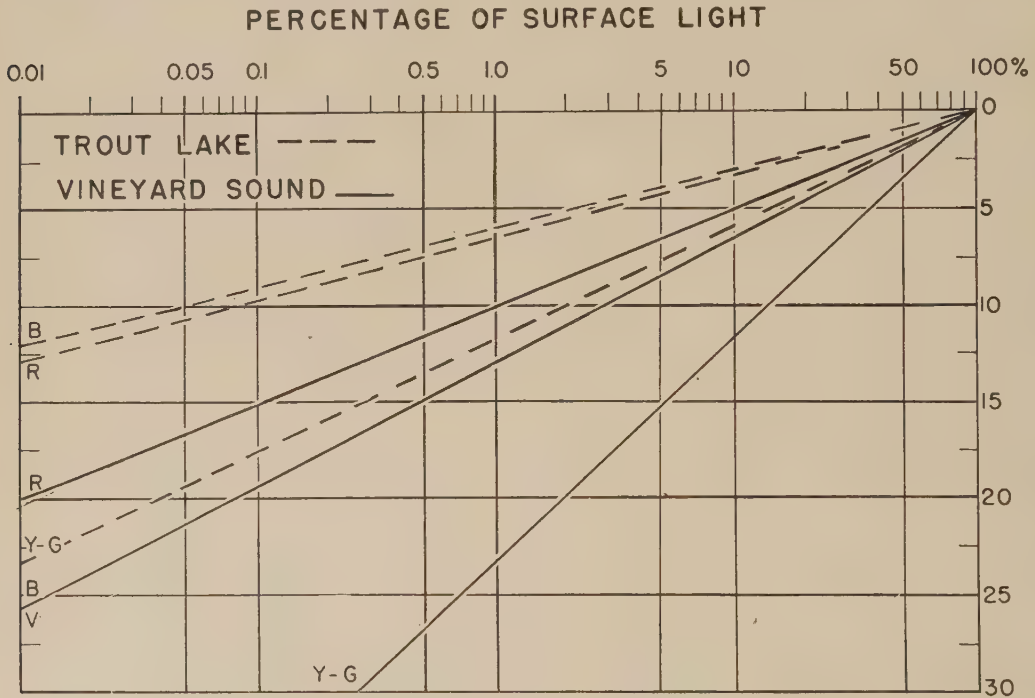


Fig. 5. Comparison of rates of penetration of four regions of the spectrum into Vineyard Sound (solid lines) and Trout Lake (broken lines). The curves represent the *average* values of the extinction coefficients as measured by Oster and Clarke (1935) for Vineyard Sound and by Birge and Juday (1930) for Trout Lake.

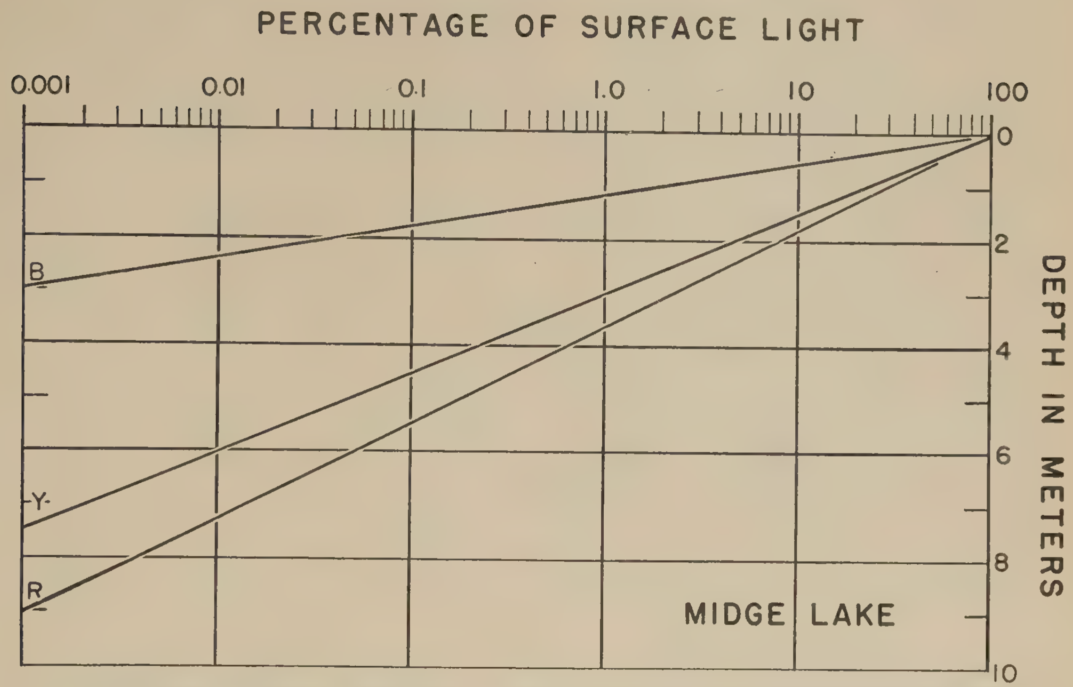


FIG. 6. Comparison of rates of penetration of three regions of the spectrum into Midge Lake. The curves represent *average* values of the extinction coefficients as measured by Birge and Juday (1930).

separate consideration will be given to the major subdivisions of the solar spectrum to which the following magnitudes may be roughly assigned: Infrared, 41 per cent; ultraviolet, 7 per cent; and visible, 52 per cent. As shown by Fig. 2, the infrared radiation is almost entirely absorbed in the uppermost meter. The chief importance of the infrared is, therefore, the rapid heating of the surface stratum.

Ultraviolet light in large amounts is injurious to plankton and other organisms,

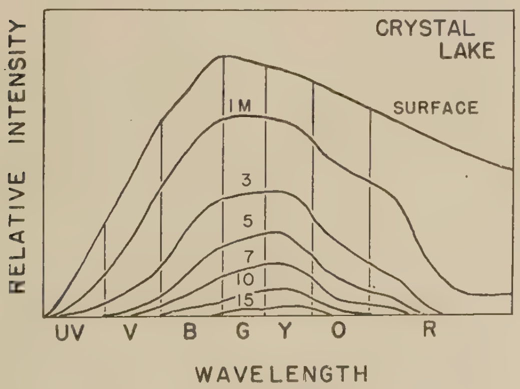


FIG. 7. Crystal Lake, Wisconsin. The spectral distribution of solar energy as it reaches the surface of the lake is given by the uppermost curve. The reduction in intensity and the changes in spectral distribution at successive depths in the lake are indicated by the curves beneath (from Birge and James 1939).

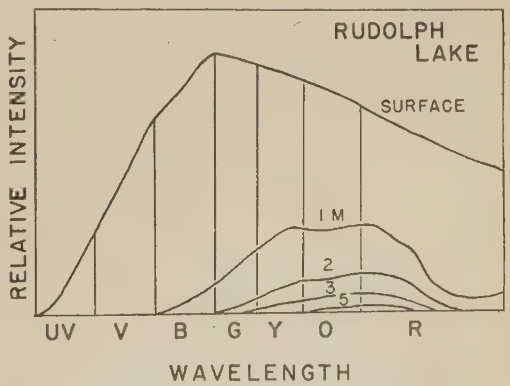


FIG. 8. Rudolph Lake, Wisconsin. The spectral distribution of solar energy as it reaches the lake's surface is given by the uppermost curve. The reduction in intensity and the changes in spectral distribution at successive depths in the lake are indicated by the curves beneath (from Birge and James 1939).

but according to ZoBell and McEwen (1935) virtually no bactericidal radiations penetrate sea water to as great a depth as 3 meters. The beneficial effects of ultraviolet in vitamin formation* and in other poorly understood ways call for exact measurements of its rate of penetration. Yet serious disagreement exists on the rate of absorption of ultraviolet light even for distilled water! In Fig. 9 the measurements of various workers at the short wavelength end of the spectrum are compared. Previously it had been supposed that ultraviolet was absorbed very rapidly by pure water itself, but the observations of James and Birge (1938) indicate a much lower absorption at least as far as 3600Å. It is essential to know whether this low rate

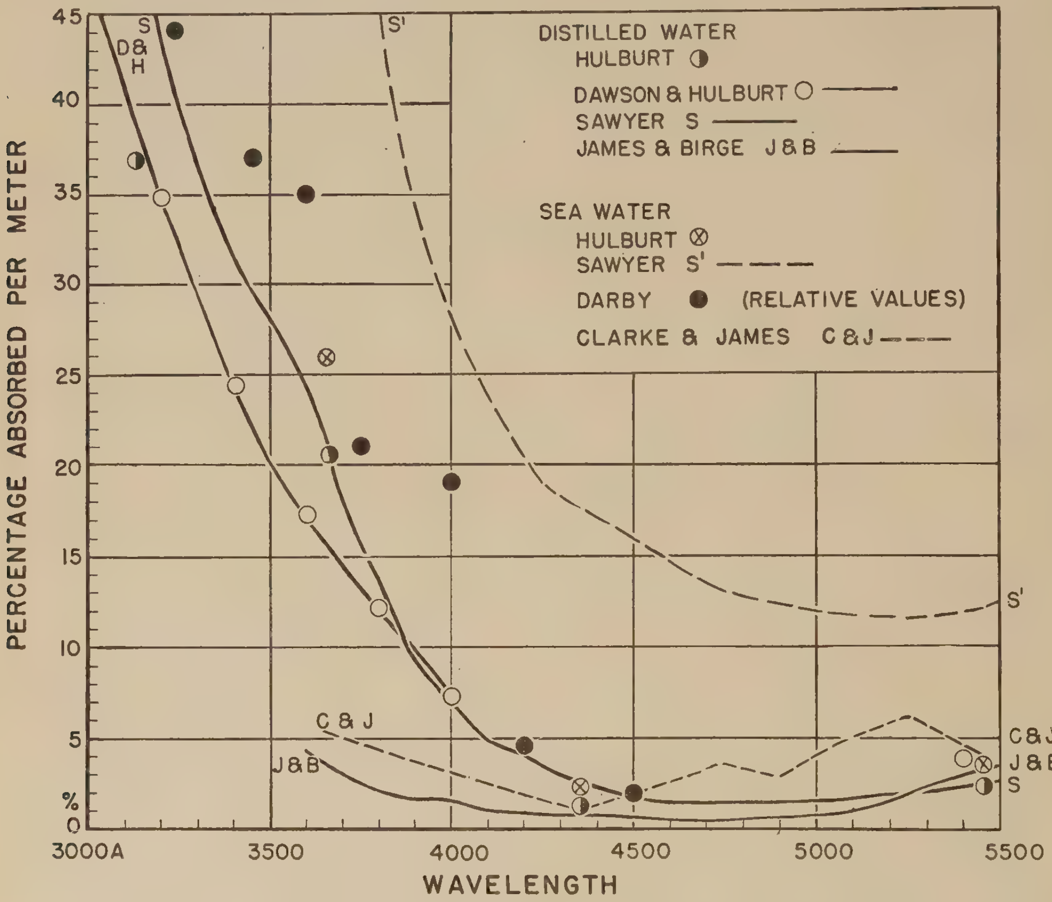


FIG. 9. Absorption of light by distilled water and by sea water at the ultraviolet end of the spectrum. Distilled water: Hulburt (1928); Dawson and Hulburt (1934); Sawyer (1931); and James and Birge (1938). Sea water: Hulburt (1928), from calculated values at 3130Å (87.8 per cent) and at 3660Å (25.9 per cent) and from data of Abbott, Fowle and Aldrich at 4360Å and at 5460Å (sea water from Caribbean agreed with these values); Sawyer (1931), laboratory measurement of water from Bay of Fundy off Head Harbor; Darby, Johnson, and Barnes (1937), relative values obtained at sea near Tortugas Laboratory, Gulf of Mexico; Clark and James (1939), laboratory measurement of water from Sargasso Sea after Berkefeld filtering.

---

* Darby and Clarke (1937) report a relatively high concentration of vitamin D in *Sargassum* and they suggest that the vitamin finds its way into cod liver oil from this source through the connecting links of a food chain. The steps involved in this suggestion should be carefully worked out since it calls for a transfer through living agents of material from the very warm Sargasso water to the cold habitat of the cod.

continues to hold for the shorter, and more important, wavelengths or whether there is an abrupt upward turn. A similar disparity is to be found among the few measurements which have been made of natural waters (*cf.* Clarke and James 1939) due largely to the lack of a sensitive instrument suitable for field use. The exact determination of the rate of penetration of this important type of radiation is thus a matter which urgently needs attention.

Turning now to the visible component of the spectrum, we find that many observations exist on the degree of activity of fish and of plankton animals in relation to its intensity. The information obtained, however, has not yet been adequately applied to the ecological relationships of the species concerned. A prominent case in point is the diurnal migration of plankton. Although research in this field has shown conclusively that the daily change in illumination is primarily responsible for the migration, the internal physiological reactions which control direction and speed of swimming are poorly understood (Welsh 1938). Even less clear are the reasons why the vertical migration of one species differs from that of another and why the behavior of the same species varies profoundly from time to time and from place to place (Clarke 1934, Kikuchi 1938, and Johnson 1938). Nevertheless the stratification of 200 plankton, which results from these reactions to light, is an aid to the investigation of certain important problems such as the feeding of these animals and their role as food for fish.

According to a recent calculation (Clarke 1936b) sufficient illumination for vision in at least one species of fish exists at the bottom in those lakes and coastal oceanic areas whose transparencies have been measured. The minimum illumination required by other species should be similarly tested and the information applied to all types of natural waters. Since the spectral distribution of the light at only moderate depths differs so materially from that at the surface, careful testing of the spectral sensitivity of the various species is imperative. The light receptors of some organisms must be exceedingly sensitive since Waterman, Nunnemacher, and Clarke (1939) have recently demonstrated a distinct diurnal migration of plankton at depths as great as 800 meters in the ocean. New information on the possibilities of vision for fish will have valuable applications to fisheries problems. It should be feasible to determine generally the depth and time of day when feeding requiring vision is possible, on the one hand, and when fish nets might be perceived and avoided on the other. The distance could be ascertained at which a submerged light is visible and its effect in attracting or repelling various types of fish.

The intensity of illumination controls photosynthesis and hence limits the depth of growth of both bottom-living and pelagic plants. For example, the lower limits for fixed plants in the following oceanic areas are:* in Baltic, 20 meters; off Iceland, 50 meters; and in Mediterranean, 130–160 meters. In lakes the lower limits are:† Trout Lake, 10–12 meters; Crystal Lake, 15–20 meters; and in Crater Lake, 12 meters. The maximum abundance of phytoplankton has been reported at the following depths:* off Syracuse, 50 meters; off California, 25–55 meters; and in north European waters, 10–30 meters. At these depths most of the radiant energy present is in the green or blue, but red light is most effective for photosynthesis (Manning 1938). Diatoms and other algae appear, however, to be able to use other parts of the visible spectrum effectively (Stanbury 1931). The mechanism which makes this possible requires elucidation.

The relative rates of photosynthesis at various levels beneath the surface have been investigated by measuring the oxygen evolved by phytoplankton placed in bottles and suspended at different depths. Near

* From Marshall and Orr (1928).

† From Juday (private communication). See also Juday (1934) and Hasler (1938). In lakes both fixed and planktonic plants have frequently been reported at depths far too great for photosynthesis. These plants must either be in a dormant or dying condition or else are living saprophytically (*cf.* Kozminski 1938).

the surface the illumination has sometimes been found sufficiently strong to inhibit photosynthesis, although the exact explanation for this is wanting (Clarke 1936a and Riley 1938). Below the point of maximum photosynthesis the rate drops off to a depth at which no appreciable reaction takes place, but respiration continues at all levels to which living cells may be distributed. The intensity of light at which photosynthesis just balances respiration is termed the compensation intensity, the value of which has been reported in two recent investigations as 500 lux and 350 lux (or 0.3 per cent of noon sunlight) respectively (Pettersson, Höglund, and Landberg 1934, Pettersson 1938, and Jenkin 1937). Since the compensation intensity will naturally vary from species to species, further determinations for types important ecologically are seriously needed. The depth at which the compensation intensity is found, known as the compensation point, has been located (for short intervals) in a number of cases:* Sargasso Sea, greater than 100 meters; English Channel, 45 meters; Gulf of Maine, 24–30 meters; East Sound (W. coast of Canada), 10–19 meters; Trout Lake, Wis., 8–16 meters; Woods Hole Harbor, 7 meters. The depth of the compensation point over an average 24 hour period is, however, the significant value from the point of view of the continued growth and ecological role of each species. Marshall and Orr (1928), working in the Clyde Sea area, found that on this basis the depth varied from 2 meters to 30 meters according to the season. Further observations from this angle in other areas are obviously of the greatest importance. There appear to be no determinations of the compensation point for 24 hours for lakes!

The productivity of any body of water depends ultimately upon the efficiency with which the plants can transform radiant energy into the potential energy of organic tissue. Kozminski (1938) attempted to approach this problem by measuring directly the quantity and distribution of chlorophyll in lakes, but found that the measurements failed to give an exact index of the mass of the phytoplankton or of the intensity of photosynthesis because of the presence of inactive chlorophyll. He states, however, that “when it is possible to measure photosynthetically active chlorophyll only, this will be the best measure of productivity.”

Another method of approach to this problem is the calculation of the quantity of carbohydrate produced on the basis of the amount of oxygen evolved by plant cells suspended in hanging bottles. Of the various experiments conducted by Manning *et al.* (1938) in Wisconsin lakes the highest quantum efficiency observed was .05. Since this value is so much lower than the value of .25 obtained by Warburg and Negelein (1923) in the laboratory, investigation of this discrepancy is demanded. Elsewhere Manning* has calculated on the basis of the average abundance of chlorophyll in a series of lakes that from 1.6 per cent to 14 per cent of the light incident on the lake is absorbed by the chloroplasts of the phytoplankton. An average value for the quantum efficiency under natural conditions according to Manning is .012 which is equivalent to an efficiency for photosynthesis of 2.7 per cent. When the two factors are taken together, we obtain:

Incident light absorbed		Efficiency of photosynthesis		Efficiency of production
min. 1.6%	×	2.7%	=	.043%
max. 14 "	×	2.7"	=	.38 "

The efficiency with which aquatic algae manufacture carbohydrate is, therefore, only a small fraction of a per cent. And not all of this product would be found in the tissues of the plant because a large part of it is consumed concomitantly in respiration and other life processes.

It thus appears that most of the light

---

* From Pettersson, Höglund and Landberg (1934), Clarke (1936a), Jenkin (1937), and Manning, Juday and Wolf (1938).

* “Photosynthesis in relation to light penetration into lake waters.” Symposium of Hydrobiology. Joint meeting of the Limnological Society of America and the American Society of Zoologists, Indianapolis, Ind., December 30, 1937.

incident on the surface of lakes or oceanic areas is absorbed by the water itself or by detritus and that only a very small part can be utilized by plants or animals. We conclude that aquatic organisms are existing under very unfavorable circumstances in regard to the utilization of solar energy. It is for this reason that the intensity, amount, and composition of the light are so frequently found to be limiting or highly significant factors in the aquatic environment. Attack on the unsolved problems outlined above is therefore urgent, and the extension of our present observations into other bodies of water and particularly over longer periods of time is of the greatest importance.

SUMMARY

The amount and nature of daylight in natural waters depends upon the surface loss, the selective absorption of the water itself, and the selective action of particulate and dissolved material. Further changes in the illumination result from differences in transparency with depth and with the season, differences in the length of day, and differences in the angular distribution of the light.

The biological significance of ultraviolet in natural waters is in doubt, but the visible component of light is important in the regulation of the activity of many animals, in the vision of fish, and especially in the photosynthesis of the plants. Since the utilization of light is very low even under the most favorable circumstances, it is understandable that light is so frequently a limiting factor in the aquatic environment.

REFERENCES CITED

ATKINS, W. R. G. and POOLE, H. H. 1933. The Photo-electric Measurement of the Penetration of Light of Various Wave-Lengths into the Sea and the Physiological Bearing of the Results. *Phil. Trans. Roy. Soc. London*, Ser. B, 222: 129.

BIRGE, E. A. and JUDAY, C. 1929–32. Solar Radiation and Inland Lakes. *Trans. Wis. Acad. Sci.* 1st Report, 24, 509, 1929; 2nd Report, 25, 285, 1930; 3rd Report, 26, 383, 1931; 4th Report, 27, 523, 1932.

BIRGE, E. A. and JAMES, H. R. 1939. *Trans. Wis. Acad. Sci.* (In preparation.)

CLARKE, G. L. 1933. Observations on the Penetration of Daylight into Mid-Atlantic and Coastal Waters. *Biol. Bull.*, 65: 2, p. 317.

————. 1934. Factors Affecting the Vertical Distribution of Copepods. *Ecological Monographs*, 4: 530.

————. 1934. Further Observations on the Diurnal Migration of Copepods in the Gulf of Maine. *Biol. Bull.*, 67: 432.

————. 1936a. Light Penetration in the Western North Atlantic and its Applications to Biological Problems. Rapports et Proces-Verbaux. Con. Perm. Intern. Exp. Mer., 101 (pt. 2): 3.

————. 1936b. On the Depth at Which Fish Can See. *Ecology*, 17: 452.

————. 1938a. Seasonal Changes in the Intensity of Submarine Illumination off Woods Hole. *Ecology*, 19: 89.

————. 1938b. Light Penetration in the Caribbean Sea and in the Gulf of Mexico. *J. Marine Res.*, 1: 85.

————. 1939. Variation in the Transparency of Three Areas of the Atlantic Throughout the Year. *Ecology*. (In press.)

CLARKE, G. L. and JAMES, H. R. 1939. Laboratory Analysis of the Selective Absorption of Light by Sea Water. *J. Opt. Soc. Am.*, 29: 43.

DARBY, H. H. and CLARKE, H. T. 1937. The Plant Origin of a Vitamin D. *Science*, 85: 318.

DARBY, H. H., JOHNSON, E. R. F. and BARNES, G. W. 1937. Studies on the Absorption and Scattering of Solar Radiation by the Sea. Spectrographic and Photoelectric Measurements. *Carnegie Inst. Wash. Publication* 475, 191.

DAWSON, L. H. and HULBURT, E. O. 1934. The Absorption of Ultraviolet and Visible Light by Water. *J. Opt. Soc. Am.*, 24: 175.

ERIKSON, H. A. 1933. Light Intensity at Different Depths in Lake Water. *J. Opt. Soc. Am.*, 23, 170.

HASLER, A. D. 1938. Fish Biology and Limnology of Crater Lake, Oregon. *J. Wildlife Management*, 2: 94.

HULBURT, E. O. 1928. The Penetration of Ultraviolet Light into Pure Water and Sea Water. *J. Opt. Soc. Am. and Rev. Sci. Inst.*, 17: 15.

JAMES, H. R. and BIRGE, E. A. 1938. A Laboratory Study of the Absorption of Light by Lake Waters. *Trans. Wis. Acad. Sci.*, 31: 1.

JENKIN, P. M. 1937. Oxygen Production by the Diatom *Coscinodiscus excentricus* Ehr in Relation to Submarine Illumination in the English Channel. *J. Mar. Biol. Ass.*, 22: 301.

JOHNSON, N. G., and LILJEQUIST, G. 1938. On the Angular Distribution of Submarine Daylight and on the Total Submarine Illumination. *Svenska Hydrografisk-Biologiska Kommissionens Skrifter Ny serie, Hydrografi*, 14: 3.

JOHNSON, W. H. 1938. The Effect of Light on the Vertical Movements of Acartia clausi (Giesbrecht). *Biol. Bull.*, 75: 106.

JUDAY, C. 1934. The Depth Distribution of Some Aquatic Plants. *Ecology*, 15: 325.

KIKUCHI, K. 1938. Studies on the Vertical Dis tribution of the Plankton Crustacea. II. The Reversal of Phototropic and Geotropic Signs of the Plankton Crustacea with Reference to the Vertical Movement. Records of Oceanographic Work in Japan, 10: 17.

Kozminski, Z. 1938. Amount and Distribution of the Chlorophyll in Some Lakes in Northeastern Wisconsin. *Wis. Acad. Sci.,* 31: 411.

Manning, W. M. 1938. Photosynthesis. *J. Physical Chem.,* 42: 815.

Manning, W. M., Juday, C. and Wolf, M. 1938. Photosynthesis of Aquatic Plants at Different Depths in Trout Lake, Wisconsin. *Wis. Acad. Sci.,* 31: 377.

Marshall, S. M. and Orr, A. P. 1928. The Photosynthesis of Diatom Cultures in the Sea. *J. Marine Biol. Ass.,* 15: 321.

Oster, R. H. and Clarke, G. L. 1935. The Penetration of the Red, Green, and Violet Components of Daylight into Atlantic Waters. *J. Opt. Soc. Am.,* 25: 84.

Pettersson, H. 1934. Scattering and Extinction of Light in Sea-Water. *Goteborgs kungl. vetenskaps—och vitterhets—samhalles handlingar.* Femte foljden. Ser. B., Band 4, No. 4, 3.

————. 1938. Measurements of the Angular Distribution of Submarine Light. Rapports et Proces-Verbaux. *Conseil Perm. Internat. pour l'Exp. de la mer.,* 108 (pt. 2): 9.

Pettersson, H. and Landberg, S. 1934. Submarine Daylight. *Goteborgs kungl. vetenskaps—och vitterhets—samhalles handlingar.* Femte foljden. Ser. B, Band 3, No. 7, 4–13.

Pettersson, H., Höglund, H. and Landberg, S. 1934. Submarine Daylight and the Photosynthesis of Phyto-plankton. *Goteborgs kungl. vetenskaps — och vitterhets — samhalles handlingar.* Femte foljden. Ser. B, Band 4, No. 5, 3–17.

Poole, H. H. 1938. The Effect of Surface Conditions on the Intensity and Angular Distribution of Submarine Daylight. Rapports et Proces-Verbaux. *Conseil perm. Internat. pour l'Exp. de la mer.,* 108 (pt. 2): 2.

Powell, W. M. and Clarke, G. L. 1936. The Reflection and Absorption of Daylight at the Surface of the Ocean. *J. Opt. Soc. Am.,* 26: 111.

Riley, G. A. 1938. Plankton Studies. I. A Preliminary Investigation of the Plankton of the Tortugas Region. Sears Foundation, *J. Marine Research,* 1: 335.

Sawyer, W. R. 1931. The Spectral Absorption of Light by Pure Water and Bay of Fundy Water. *Contr. Can. Biol. Fisheries,* N. S., 7: no. 8, 75.

Stanbury, F. A. 1931. The Effect of Light of Different Intensities, Reduced Selectively and Non-selectively upon the Rate of Growth of Nitzschia closterium. *J. Mar. Biol. Ass.,* N. S., 17: 3, 633.

Utterback, C. L. and Jorgensen, W. 1934. Absorption of Daylight in the North Pacific Ocean. *J. Conseil. Int. l'Exp. de la Mer.,* 9: 197.

Warburg, O. and Negelein, E. 1923. Ueber den Einfluss der Wellenlänge auf den Energieumsatz bie der Kohlensäure-assimilation. *Z. Physik. Chem.,* 106: 191.

Waterman, T. H., Nunnemacher, R. F., Chace, F. A., Jr. and Clarke, G. L. 1939. Diurnal Vertical Migration of Deep Water Plankton. *Biol. Bull.,* 76: 256.

Welsh, J. H. 1938. Diurnal Rhythms. *Quarterly Review Biology,* 13: 123.

Whitney, L. V. 1938a. Microstratification of Inland Lakes. *Trans. Wis. Acad. Sci.,* 31: 155.

Whitney, L. V. 1938b. Transmission of Solar Energy and the Scattering Produced by Suspensoids in Lake Waters. *Trans. Wis. Acad. Sci.,* 31: 201.

Whitney, L. V. 1939. (In preparation.)

Zobell, C. E. and McEwen, G. F. 1935. The Lethal Action of Sunlight upon Bacteria in Sea Water. *Biol. Bull.,* 68: 93.

Contribution No. 202

Reprinted from THE JOURNAL OF EXPERIMENTAL ZOOLOGY
Vol. 81, No. 3, August, 1939

THE PHYSIOLOGY OF COLOR CHANGE IN FLATFISHES [1, 2, 3]

CLINTON M. OSBORN [4, 5]
Biological Laboratories, Harvard University, Cambridge, Massachusetts

THREE PLATES (NINETEEN FIGURES)

Since the classical experiments of Pouchet (1872, 1876), numerous investigators have reported evidence for the nervous control of fish chromatophores.

K. v. Frisch ('11), Spaeth ('16, '18), Gianferrari ('22), Wyman ('24), Abolin ('25), Hewer ('25, '27), Gilson ('26), Scharrer ('28), Kropp ('29), Giersberg ('30, '32), Meyer ('31), Fries ('31), Smith ('31 a, '31 b), Odiorne ('33), Parker ('34 a), Kleinholz ('35), Abramowitz ('36, '37), Veil ('37), Osborn ('38) and Matsushita ('38), all have recorded observations concerning endocrine influence in teleost color change. Although these investigators worked with various species of fishes and their conclusions were not entirely harmonious, they do show that the secretions of certain endocrine glands, namely the hypophysis, the adrenals and possibly the epiphysis, may be functional in chromatic changes.

---

[1] This work was aided in part by a Bache Fund grant administered by Prof. G. H. Parker.

[2] Contribution no. 202 of the Woods Hole Oceanographic Institution.

[3] Parts of these investigations were carried out at the Woods Hole Oceanographic Institution and the Marine Biological Laboratory, Woods Hole, whose staffs together with that of the U. S. Bureau of Fisheries were cooperative in collecting fishes for my use.

[4] Parker Fellow in Biology at Harvard University.

[5] I wish to express my appreciation to Prof. G. H. Parker, whose many kindnesses throughout the course of this work aided materially in making it possible. I am also grateful to Profs. A. B. Dawson and F. L. Hisaw and Dr. A. A. Abramowitz for reading the manuscript and making suggestions and to my volunteer assistant, Mr. Gordon French, for aiding in the routine work.

It is now generally accepted that color changes in many teleosts are produced normally by the combined actions of nerves and endocrine substances. For the most part it is not yet clear whether fish chromatophores are singly or doubly innervated or how many different internal secretions may act upon the effectors of a particular species. Moreover, the relative significance of nerves and internal secretions varies among species. Fundulus depends chiefly upon nervous control, reinforced in the circulation by a melanophore-dispersing pituitary substance which is allowed expression primarily in denervated experimental areas (Kleinholz, '35; Abramowitz, '37). This secretion is probably of little significance in the normal color change of this animal except perhaps insofar as it provides an environment in which controlling nerves may function more effectively. In the catfish, however, a pituitary secretion is important in producing the dark state and serves as a controlling mechanism in conjunction with other humoral and nervous agents (Parker, '34 a; Abramowitz, '36; Veil, '37; Wykes, '37; Osborn, '38). Smith ('31 b) in Phoxinus and Abramowitz ('36) and Osborn ('38) in the catfish have found evidence for the paling action of an adrenalin-like substance associated with excitement. Because of recent advances which indicate that the mechanisms of teleost chromatology are more complex than was formerly appreciated it seemed of interest to reinvestigate the physiology of color change in the flatfishes, certain species of which were shown to be highly adaptive to shade, color and even pattern by the outstanding researches of Sumner ('11) and Mast ('14). The former investigator worked mostly with Mediterranean turbots, Rhomboidichthys podas, Rhombus maximus and Rhombus laevis and the common sand dab, Lophopsetta maculata, native to Woods Hole. Mast's experiments were confined for the most part to Paralichthys albiguttus and Ancylopsetta quadrocellata.

In this preliminary report, experiments on the winter flounder (Pseudopleuronectes americanus), the summer flounder (Paralichthys dentatus) and the sand dab (Lophopsetta maculata) are presented which indicate the relative functions of nervous and non-nervous agents in the chromatic behavior of these representative flatfishes. Since the majority of experiments were done with winter flounders, due to their relative abundance, the greater part of the discussion will concern this species.

MATERIALS AND METHODS

The fishes were taken in traps or by otter-trawl from the waters about Woods Hole and were kept in large stock tanks in which the environment was quite natural. Wooden tanks about 2 feet square with sides 18 inches high, painted inside with photographic black or flat white, were used for background adaptation. One 100 watt lamp placed 18 inches above each tank provided constant illumination.

Frequent cleaning and replacement with freshly painted tanks assured pure black or white backgrounds. The tanks were supplied with running sea water at 19° to 20°C. In most cases, only a single fish occupied a tank at one time to avoid the possibility that additional fishes might render the environment qualitatively uncertain. The animals were fed regularly with minced clams or squid.

Although most operations were performed without anesthesia, some fishes were stupified with ice water (Parker, '38). Animals were totally blinded either by section of the optic nerves or by complete optic enucleation. Areas were denervated by operations similar to those used by Pouchet (1876), Wyman ('24) and others. A photographic darkroom was used for all experiments done in total darkness.

The tetanizing current used in electrical stimulation was supplied by a simple induction coil in series with a tap switch and dry cell. The stimulus used was of 'strong' intensity as judged by touching the electrodes to the tip of one's tongue (2 minutes of steady stimulation never killed a fish). The fish, in air, was placed upon one electrode (zinc plate) while the other electrode was placed either in the mouth or on the side of the head. Other exciting stimuli were: 1) mechanical

—handling or prodding with a rubber tipped rod or 2) visual —the approach of the observer or waving the hand over the tank.

Photographs of all significant responses were made under constant conditions. The comparative study of many series of photographic enlargements has made it possible to follow the chromatophore responses to various stimuli in any given area of the integument.

EXPERIMENTAL

A. Adaptation to constantly illuminated backgrounds

White. When winter flounders are transferred to white from a natural background, appreciable paling occurs in a few minutes to half an hour but complete blanching requires 3 to 7 days. This might be called the 'primary' stage of paling (caused by actual concentration of melanophore pigment) for further slow paling will occur which reaches an apparent maximum in 3 to 4 weeks. This 'secondary' lightening is mainly due to melanophore degeneration accompanied by guanophore production and results in a very white fish (fig. 5). The characteristic black spots show considerable variation in their responses but ordinarily disappear in a few hours to 1 day but usually reappear if the fish is undisturbed. If the fishes have previously been black-adapted (just adapted —not a long stay) they pale according to the same schedule but a much longer time is required if the sojourn on black has been sufficient to cause excessive melanin production. The initial changes in shade from black to slate gray occur in a very few minutes.

The summer flounder adapts more quickly to white than does the winter flounder (figs. 19 A to 19 H). When placed on white directly from nature, the fish adapts noticeably in from 1 to 5 minutes but is not well adjusted until from 2 to 4 days (figs. 19 H), after which it continues to whiten by melanin degeneration and guanophore multiplication. The animal may become very white in 6 to 14 days. The positions of the black spots are always apparent even in white animals although the spots are not obviously black. Following a 7-day stay on black, the fishes white-adapated in 42 to 48 hours. Longer periods which cause extensive quantitative changes in the pigment retard the rate of adaptation.

Sumner ('11) reported rates of adaptation for Lophopsetta to vary from a few hours to 2 or 3 days. My findings are in general agreement as I encountered animals which varied between 2 hours and 2 days (fig. 13 A). As in both other species the sand dab required more time to white-adapt following prolonged exposure to a black environment. A few individuals which had reposed on black for 3 or 4 weeks required 6 to 8 days to white-adapt again. This may explain certain cases which Sumner termed 'refractory.' His stock tank was painted black.

Black. The winter flounder adapts to black in from 3 to 5 days, somewhat faster than to white. In many undisturbed black-adapted fishes several white spots along the margin of the body become clear (fig. 11). These spots, although usually present in fishes intermediately brown (from nature) are never so distinctly obvious as in black-adapted individuals. Previous adaptation to white (7 to 25 days) retards black-adaptation to about 6 to 8 days although the first evidence of darkening (appearance of black spots) is apparent in 10 minutes.

Paralichthys dentatus becomes black-adapted in from 1 to 3 days when taken from nature and the time is not greatly increased when transferred from white unless the sojourn there has lasted several days. The undisturbed fish becomes so homogeneously black that the black spots obvious under other conditions cannot show and only remnants of white spots appear as occasional specks (fig. 19 A).

The sand dab adapts to black (fig. 12))in about 1 day when taken from nature and in 2 to 3 days if previously exposed to white for more than 1 week. Shorter exposures to white which regularly result in complete paleness do not affect the rate of adjustment to black. The initial adaptive changes shown by the sand dab to either black or white occur rapidly.

Pronounced changes are apparent in the first 2 or 3 minutes but, nevertheless, the above periods of time are needed for complete adaptation.

General considerations of background responses. Of all three species used here it may be said that the adaptation 'times' presented are for the relatively rapid physiological migration of pigment granules (dispersion or concentration) and that all the species continued to adapt more completely if longer periods were allowed. This second type of change is morphological (a quantitative change in pigment, Odiorne, '37) and probably occurs coincident with as well as subsequent to the more rapid adaptation. For this reason, it is not easy to establish an absolute endpoint and thus the 'timing' for rates of adaptation is subject to considerable error. All three species adapt well to black and white. The summer flounder and sand dab, when undisturbed, become very homogeneous in shade with only very small remnants of spots of contrasting shades indistinctly apparent. However, the winter flounder differs in that, when undisturbed, it frequently possesses black spots when white-adapted and white spots when black-adapted (figs. 1 A and 11).

Many investigators have reported an increase in the rate of adaptation to background upon repetition of the response. This is confirmed in all three species of flatfish considered here. A faster response was noted in most animals even after but one trial. For example, summer flounders which required from 1 to 3 days to adapt to black when taken from nature usually adapted to the same extent in from 15 to 20 hours on a second trial immediately following the first. After many trials, the adaptation time was sometimes reduced from days to minutes.

Besides the color responses of the general body shade, mention should be made of the behavior of the spots typical of each species. Due to the fact that they exhibit considerable variability in response, primarily because of excitatory factors, as will be seen in a subsequent section, the spots are not entirely dependable in their reactions. However, for the most part, when an undisturbed dab or summer flounder homogeneously white-adapted is transferred without excitement to a black environment, the black spots (centers of high concentration of melanin apparent only as indistinct remnants in the pale fish) quickly appear followed by a gradual general darkening of the whole integument. Again, when homogeneously black-adapted undisturbed individuals of either species are transferred without excitement to a white background, the white spots (centers of lower concentration of melanin together with high concentration of guanin, apparent only as pale remnants in the black fish) appear immediately and distinctly, followed by gradual body paling (figs. 19A to 19H). The appearance of the white spots is evidently not due to a change in guanophore size for they are fairly constant in size under all conditions, but rather to concentration of the superimposed melanophores thus exposing the reflecting layer. Whether these particular melanophores respond faster than those of the general integument or are controlled by the same or different mechanisms will be considered later.

B. Responses to darkness

The responses of sand dabs and winter flounders to total darkness were observed at frequent intervals for over a month. Notes taken during the first few hours in darkness agree in general with Sumner ('11) who used Lophopsetta. Previously white-adapted fishes when placed in darkness tend to darken slightly to a light grayish-brown and almost always dark spots appear. Previously black-adapted animals retain their dark shade for the most part but do blanch somewhat. As more time elapses in continuous darkness, both groups gradually lose their previously distinctive shades and approach a shade intermediate or slightly darker (usually a rich brown). Some dark spots usually appear. The rates at which individuals reach the intermediate shade vary considerably (between 1 and 3 weeks). The above remarks concern animals which were put on the respective backgrounds just long enough to become adapted and were then transferred to darkness. Long sojourns on black or white result in a quantitative change in pigment which is evident for several weeks in animals placed in darkness.

Denervated bands usually appear darker than the rest of the integument but occasionally are observed to be pale in contrast. However, fishes tend to be more sensitive to exciting stimuli in darkness and mild touching and handling is frequently sufficient to cause excitement pallor in denervated areas (see later section). It is also possible that the light which was flashed on several times during each recording was a sufficient stimulus to initiate pallor.

C. Behavior of blinded flounders

When pale winter flounders are totally blinded, they darken to an intermediate or darker homogeneous brown (fig. 4). They remain in this state regardless of background or degree of illumination. A few specimens observed in total darkness were also of the above described tint. Sand dabs blinded in the pale condition also assumed a medium dark shade although sometimes not until several hours elapsed. Such a delay was noted also by Sumner ('11). This species also appeared quite homogeneous in brownness. Contrasting spots were uncommon.

Either species blinded in the black-adapted condition blanched from the excitement of the operation but subsequently darkened to approximately the original shade. Although this blackness gradually mellowed to approach the shade described in the preceding paragraph, it was a very slow process and in the course of these limited experiments, the fishes never paled enough to become indistinguishable from the above group. Here again the duration of the preliminary stay on black is probably significant. It is also likely that both groups would assume the same homogeneous brownness in time. A few observations in the darkroom indicated that their behavior was not unlike that observed in light.

The outstanding points in the behavior of blinded individuals of these species seemed to be that the shade assumed was slightly darker brown than intermediate and strikingly homogeneous. Contrasting spots of dark or light shades are minimized.

DENERVATED AREAS

Since the work of Pouchet (1872, 1876) with the turbot, numerous investigators have utilized nerve section as a tool in studying color changes of amphibians, reptiles and various fishes besides the teleosts.

In the present experiments, two general types of operation have been used: 1) the sympathetic chain was cut at definite points along its course in the posterior half of the body or 2) lateral branches of the sympathetic associated with spinal nerves were cut along their lateral axes from near the lateral line to the margin of the fin. One nerve cut near the lateral line results in a slightly V-shaped darkened area extending to the periphery of the fin. At the distal end, the size of the area which varies with the size of the fish is sometimes over 1 cm. wide. A cut of the same size but more distal results in a proportionately narrower and necessarily shorter band. This is due to the fanlike spread of the innervation progressing distally.

In the denervating operations, special effort was made to sever the nerves cleanly without disturbing the circulation unnecessarily. Complete success in such an undertaking is, of course, impossible. The sympathetic chain is so intimately associated with the haemal canal that hemorrhage was not infrequent. However, only the best operations were selected for successive experiments.

All three species of the flounders used exhibit typical clean cut darkening responses to denervation, similar to those described by Pouchet. The darkening becomes apparent in a few seconds following nerve section and the affected area darkens maximally in a few minutes (figs. 6 B, 14 A and 17 A). This is clearly seen only in animals whose general shade is paler than maximum blackness. In black-adapted fishes, denervation has no effect on the immediate appearance of the area unless it has normally contained white spots. In such cases, denervation causes an immediate darkening of the spots (figs. 16 A and 16 B). This suggests that the white spots are controlled by nerves which may act in producing local paleness (white spots) despite the fact that the rest of the fish may be black. If the operated animals are kept on an illuminated white background, the black denervated area gradually fades to brown, then buff and finally practically disappears. The time reqquired for complete fading varies with the species and the size of the denervated field. Areas in the sand dab fade fastest and in the winter flounder most slowly (figs. 7 A, 8 A and 15 B). Since large portions of the posterior of the animal denervated by section of the chain do not show complete fading,[6] a consideration of bands is appropriate. A band produced by cutting one caudal or one marginal fin ray in the sand dab fades in from 1 to 4 days. A similar band in the marginal fin of the winter flounder sometimes does not fade in a week. Larger denervated areas require proportionately longer periods to fade. An area including seven rays in the marginal fin of the winter flounder was still apparent 9 weeks after the operation. A true appreciation of the fading reaction requires, of course, that the fish be not excited or disturbed during or previous to an observation. Denervated areas have been recorded as 'pale' frequently but subsequently appeared dark in white-adapted fishes. This temporary paleness was in all probability an excitement phenomenon which will be discussed later more fully. If the denervated area is observed 'pale' in a black-adapted fish there is no danger of confusing it with fading but in white-adapted animals it is easily mistaken for fading if subsequent observations are not recorded. An area to be considered faded must not be apparent in an undisturbed white-adapted fish. If a band is faded, it undergoes background changes consistent with the shade of the rest of the integument when the fish is shifted from white to black and vice versa.

---

[6] Although such areas may eventually fade, fishes observed almost 3 months after section of the chain had not faded completely. The blackness had changed to a brown and that in turn to buff.

Interpretation of the fact that denervation results in an immediate darkening has divided most investigators into two schools. Some members of the first believe the reaction is a consequence of paralysis and that in the absence of nervous continuity, the melanophores disperse their pigment under the influence of other agents which were not strong enough to express themselves in the presence of nervous connection. Others of this school believe that the dark condition is a resting one to which melanophores automatically migrate when not under nervous influence. The second school (neurohumoral) interprets the darkening as the result of vigorous nervous stimulation caused by the cutting. This stimulation is believed by the neurohumoral school to be accompanied by an excessive discharge of oil-soluble secretion at the nerve endings which actually brings about the darkening. Fading occurs when the active secretion is exhausted or when concentrating neurohumor from surrounding areas invades and overpowers the dispersing secretion. One of the strongest pieces of evidence in favor of this interpretation is that in Fundulus and the catfish the cut nerves may be reactivated (Parker, '34 a) by a second cut causing a redarkening of a previously faded area.

The winter flounders used here did not prove to be favorable material on which to test this point. In the first place, reactivation cannot be tested satisfactorily until fading is complete yet the nerves must still be functionally healthy if they are to be capable of carrying impulses. Such a combination of circumstances is not readily found in this species. In most cases fading is so slow that the nerves will have degenerated by the time the area fades sufficiently for a reliable test. However, this in itself suggests that the lingering dark area is perhaps not due to such a neurohumor for it is highly improbable that such a substance could persist in a localized area for so long a time following the original cut.

The limited attempts which were made to reactivate nerves at a time when fading had occurred and yet the nerves were probably still alive, produced no clear evidence. In a few instances some darkening was apparent but in view of the fact that similar responses, which will be discussed under "excitement responses in denervated areas," were evoked as long as 4 weeks after the original operation, it is difficult to know how to interpret these findings.

EXCITEMENT RESPONSES

These resonses vary with the strength of the stimulus and may be logically considered as they occur in innervated and denervated areas:

Normal innervation. Mild mechanical stimulation supplied by gently touching or prodding with a rubber tipper rod or visual stimulation such as the sudden approach of an observer or waving the hand over the tank resulted in the following rapid responses:

1a. The characteristic black spots on hitherto undisturbed pale winter flounders disappear, leaving the surface uniformly pale (figs. 1 A and 1 B).

1b. Any white spots present on undisturbed black-adapted winter flounders disappear, resulting in homogeneous blackness.

2a. Several irregularly shaped black spots appear on the surface of white-adapted summer flounders (fig. 19 G). Sometimes the entire surface darkens slightly.

2b. Many white spots come into view on the dark surface of black-adapted individuals of this species (fig. 18 A). The entire surface may pale very slightly.

3a. Many dark brownish-black spots appear on the surface of the fins of white-adapted sand dabs (fig. 13 D). A slightly stronger stimulus produces similar spotting throughout the pigmented surface and may result in a general slight darkening (fig. 13 E).

3b. Creamy white spots appear on black-adapted sand dabs. Sometimes they first come into view on the fins. Usually a noticeable pallor extends over the entire body surface.

These responses are of short duration starting 3 to 5 seconds after the beginning of stimulation and usually reaching a maximum in 15 or 20 seconds. If stimulation of the same strength is continued, the outcome is quite variable. The response may continue at maximum for several minutes and then disappear or the integument may immediately return to its original shade despite continued stimulation. This might be interpreted to mean that for some fishes the stimulus continues to be real and adequate while for others, perhaps less sensitive, the stimulus ceases as such when the fish becomes accustomed to it and so is no longer disturbed. This is perhaps strengthened by the fact that some individuals which have received repeated stimulation ultimately fail to respond or else require a stronger stimulus to elicit the same response.

Vigorous stimulation, for example rough handling, prodding with a needle-pointed rod, or electrical stimulation produces marked changes, the first steps of which are identical with those listed above. In addition to the first response (1a above) the entire surface darkens and takes on a rather pronounced mottled appearance (fig. 2)—black and white. Response 1b is enhanced by a general paling to a brownish gray which is quite marked. Occasionally some mottling is evident. Response 2a is increased to a marked general darkening and usually a distinct mottling (fig. 18 B) much coarser in detail than in the winter flounder. Sometimes, the mottling disappears or does not occur at all and the fish becomes homogeneous in tone but distinctly darker in shade than originally. It has been observed, however, that the mottling response is more likely to occur if previous to white-adaptation the animals are black-adapted for several days. Response 2b progresses to a homogeneous dark almost black shade often but slightly paler than the original. This involves the rapid disappearance of the white spots which initially appeared. The 3a response develops to numerous dark spots over the entire pigmented surface and a marked general darkening (to brown) of the whole surface (figs. 13 E and 15 C). The last reaction (3b) becomes somewhat enhanced to the extent of marked paling over the entire fish. A pattern of spots similar to that of 3a, but less obvious, usually appears.

These pronounced responses to vigorous stimulation last from a few minutes to one hour depending upon the individual and upon the duration of the stimulus.

It should be stated concerning the presence, appearance or disappearance of spots (black, white, etc.) that their position on the surface is never random but always constant. This is in agreement with the findings of Sumner ('11) and Mast ('14) in other flatfishes. The general shape of the spots is also constant but subject to modification by partition (being subdivided into smaller parts by the migration of pigment in superimposed melanophores). They should be thought of as fixed morphological structures insofar as they represent concentrations of pigment quite different (greater or lesser accumulations) from those in adjacent areas. The size and detailed shape of the spots vary with the degree of masking or unmasking, resulting from pigment migration. The fact that they appear or disappear so quickly in excitement also strongly suggests that they are under nervous control.

In denervated areas. Mild excitation of the fish has no apparent effect on denervated chromatophores. However, a vigorous stimulus sufficient to excite the animal thoroughly produces an interesting response which may be comparable to what has been termed by many investigators 'excitement pallor.' This part of the discussion will be limited to the winter flounder for most of these experiments were conducted on this species. Preparations were made by cutting rather wide bands through the body fin musculature to sever sympathetic fibers running out from the sympathetic chain with the spinal nerves. Usually two or three consecutive nerves with the included sympathetic fibers were cut about 1 cm. dorsal or ventral (in a 20-cm. fish) to the lateral line by an incision parallel with it. Broad bands thus prepared allowed a comparison of the behavior of chromatophores on a surface of the thicker portion of the body with those on the more transparent fin. In this way it was also possible to cut several bands on the same fish and thus afford a comparative observation of bands of different sizes and ages and avoid individual differences in fishes. The general appearance, fading, and adaptive behavior of such areas has been presented in a previous section.

If a black-adapted fish possessing such a band at least 1-week old is vigorously stimulated by any of the previously mentioned methods, the denervated area becomes pale (fig. 9) while the reactions of the innervated integument take place as described on page 491. This paling of the denervated area reaches a maximum in 3 to 5 minutes and may last from 20 minutes to 3 or 4 hours, depending upon the duration and strength of the stimulus and upon the individual animal. A detailed account of the sequence of events is as follows: Before an exciting stimulus, the entire integument (innervated and denervated areas alike) is homogeneously black. Then an electrical stimulus is applied for 1 minute. After the first few seconds of excitement, any white spots present disappear and the whole innervated integument pales appreciably with the result that the denervated band stands out in dark contrast. This no sooner appears as a dark band than it begins to pale. The first evidence of paling becomes apparent in 15 seconds to 1 minute, frequently at the edges of the denervated area. Although the paling frequently occurs first at the lateral and proximal edges and progresses centripetally, finally to obliterate the last trace of dark along a central line, in other cases it spreads uniformly over the entire denervated area. In either event, the whole area (five to seven fin rays) attains maximum pallor in 3 to 5 minutes. This paleness is much more pronounced than that of the rest of the fish which by this time is redarkening, having passed its maximum paleness. Qualitatively, the paling of a denervated area in any given fish is quite constant. An area paling evenly does so in every repeated trial while in another fish a centripetal paling is always characteristically repeated. This suggests that the difference between individuals may be due to slight variations in circulatory obstructions at the time of the original operations, followed by differencs in the reestablishment of circulation by collateral compensation and the regeneration of some of the severed vessels. This paling reaction has been elicited repeatedly in a denervated area (seven fin rays) on the same fish from 6 or 7 to 70 days after denervation. At the end of this period only partial nervous regeneration had occurred. A large percentage of the original area was still denervated. The apparent slowness of regeneration is undoubtedly due to the size of the area denervated which originally measured about 4.5 cm. by 1.6 cm.

The paling response of such denervated areas obviously cannot be due to the direct action of nerves. Moreover, it seems unlikely that oil-soluble neurohumors secreted at nerve endings in adjacent areas as Parker ('34 a, '35 a and b) has described in catfish, certain elasmobranchs and Fundulus, could produce this relatively rapid response. Lipohumors, as described by Parker, act in changing the shade of a denervated area by slow cell to cell diffusion which may require a few hours to darken a single-ray band in the catfish. Concentrating neurohumors as reported in the elasmobranchs are apparently of similar slow action. Furthermore these substances characteristically invade the periphery first and slowly advance centripetally. Apparently they never bring about a uniform change over the whole denervated surface at one time. For these reasons it seems that the active concentrating substance under discussion is not an oil-soluble neurohumor but is in all probability blood borne. Immediately such substances as adrenalin, acetylcholine and sympathin come to mind. Data bearing on these possibilities are presented in a later section but before passing to these considerations, indirect evidence on the significance of circulatory continuity in ensuring homogeneous pallor in a denervated area should be presented.

If in a seven-ray band such as that in the above detailed account, the middle ray is cut any time after 10 days subsequent to the original operation, a narrow dark band appears distal to the cut in 10 or 15 minutes (fig. 10). The band is not black but clearly darker than the surrounding denervated band which becomes pale from excitement. The narrow band was not apparent when the fish was excited again 16 hours later, but upon recutting slightly distal to the previous cut, it reappeared faintly within 20 minutes. This in turn was very faint 2½ hours later and could not be discerned upon further excitement of the fish 6 hours later. The production of a dark band by a new cut within a faded denervated area has been accomplished as long as 4 weeks after the original operation. Longer periods have not been attempted. Dark secondary bands so produced are probably unlike those obtained in the catfish (Parker, '34 a) and the smooth dogfish (Parker, '36). These latter bands have been interpreted as due to a reactivation of nerves present and still functional in a band previously denervated but a few days. According to Parker, reactivation is impossible in older bands because of degenerative changes [7] in the nerves. Such observations have been used in support of the neurohumoral theory. In the experiments presented here, however, degenerative changes have in all probability occurred at least in 3 or 4 weeks and thus in the absence of active nerves from the area there is little left to consider other than circulatory disturbance. Such a cut would necessarily result in some temporary vascular congestion despite the fact that circulation in the area appeared under the microscope to be plentiful. Any cut across a fin ray must sever some blood vessels and result in an area in which circulation is not normal even though it may be plentiful for the nourishment of the tissues. It may be then that any concentrating substance in the circulation of the originally denervated area is unable to reach the melanophores of the second band in normal quantities to maintain the pale condition there. What the positive reason may be for the darkening in the new band is not clear. This matter has been brought up only to show that secondary cuts may produce dark bands in denervated areas which must in all probability contain only degenerated nerves.

---

[7] Degeneration was found to reach completion in the nerves of denervated caudal bands of Fundulus about 12 days after cutting (Parker, '34 b, p. 314).

EFFECTS OF INJECTIONS OF ADRENALIN

Adrenalin effects in teleosts are in general uniform and so well known that any detailed discussion is unnecessary. Doses ranging from 0.05 to 2.0 cc. of 1:10,000 adrenalin chloride (Parke, Davis and Co.) have been injected intramuscularly and intraperitoneally with resulting homogeneous pallor over the entire body. Some of the lower dosages produced only very slight or local responses. In general all three species responded alike but occasionally the summer flounder and sand dab showed mild mottling not apparent in the winter flounder.

Denervated areas in all the species are much more sensitive than innervated areas and exhibit paleness for an appreciable time after the rest of the fish has returned to the black-adapted condition. Furthermore, in the winter flounder, low doses were found which caused but slight general paling but produced marked blanching in denervated areas. It is interesting that responses in denervated bands of the winter flounder which were apparently identical to those caused by vigorous excitement have been produced by adrenalin. The fact that the responses to both stimuli seemed identical to the observer does not necessarily prove that adrenalin is the active agent in the circulation of excited fishes. Furthermore the process of injection is occasionally sufficient to produce the pallor response although usually this is not the case.

Adrenalin injections were as effective in blanching the entire posterior portion of a fish (denervated by section of the sympathetic chain) as in paling denervated bands (figs. 17 A and 17 B). However, because the circulation posterior to the point of section is frequently impaired, it is easy to understand why adrenalin injection in such animals usually fails to produce homogeneous pallor throughout the denervated region (figs. 14 B and 14 C). Instead, those areas where circulation is normal blanch first, followed logically by other areas where congestion makes it more difficult for the adrenalin to reach the effectors. However, if several days elapse after the chain is sectioned, allowing circulation to be reestablished throughout the region, the denervated effectors respond uniformly to adrenalin injection. Their behavior is quite comparable to that of bands. Generally speaking, vigorous excitement produces the same effects as adrenalin in areas denervated by section of the sympathetic chain—effects identical with those described above for bands. The large areas were not preferred for study, however, because of the more serious uncontrollable factor of circulatory disturbance.

EFFECTS OF INJECTIONS OF MELANOPHORE-DISPERSING SUBSTANCES OF THE PITUITARY

In these experiments, the winter flounder was always the recipient of the injection made either subcutaneously or intraperitoneally and the melanophore-dispersing material was one of four preparations: 1) a suspension of finely ground fresh pituitaries of the summer flounder;[8] 2) a relatively more pure and concentrated extract of summer flounder pituitaries;[9] 3) obstetrical, pituitrin (Parke, Davis and Co.); 4) a very concentrated extract of intermedin prepared chemically from fresh sheep pituitaries.[10] All of these preparations were standardized on white-adapted frogs or on both frogs and white adapted catfish.

[8] These fishes were caught for commercial use and were kept on ice constantly until unloaded at the wharf. There the pituitaries were obtained as soon as the heads were discarded. Although the pituitaries varied in size, the fishes from which they were taken averaged about 8 pounds. The recipients (winter flounders) weighed about 1/15 as much.

[9] Acetone-dried glands were powdered. The powder was taken up in distilled H_2O made alkaline with NaOH and this was brought to a boil. The solution was neutralized to litmus with HCl. Sufficient 95% alcohol was added to bring the entire solution to 80% alcoholic. The precipitate was discarded. The alcohol was evaporated off from the supernatant and the resultant active material was taken up in distilled H_2O for injection.

[10] Intermedin was obtained through the kindness of Dr. A. A. Abramowitz.

Minced pituitaries.[11] Two pituitaries were sufficient to cause a very slight darkening in test frogs. However, doses as high as ten summer flounder glands failed to affect the shade of white-adapted winter flounders. Extracted summer flounder pituitaries—the equivalent of two pituitaries produced a greater darkening than was obtained above but the response was not marked. Three pituitaries produced a good darkening which lasted over 5 hours. The equivalent of three pituitaries darkened test catfishes just perceptibly but twelve pituitaries caused pronounced darkening which lasted over 12 hours. Similar doses evoked no response in test winter flounders.

Pituitrin. Injections of as much as ½ cc., sufficient to produce pronounced blackness in test frogs and catfishes, failed to affect the shade of recipient winter flounders.

Intermedin. Very small doses of this concentrated extract were capable of darkening frogs to almost black. The response usually lasted between 24 and 36 hours. The same dose would cause a marked darkening response in test catfishes but would wear off in about 18 hours. Starting at this level, the dosage was increased gradually until the highest doses were fifty times as great. Even then, no appreciable response was observed in winter flounders.

Effect of melanophore-dispersing substances on denervated areas. All the above groups of winter flounders contained individuals with relatively faded denervated areas. However, darkening was no more apparent in the denervated areas than has been reported for the rest of the integument.

EFFECTS OF OTHER DRUGS

Nicotine. Preliminary experiments involving intramuscular injections of nicotine into winter flounders indicate that doses which are lethal or just sublethal caused a pronounced darkening (figs. 3 A and 3 B) which lasted as long as 18 hours in some fishes which survived.

---

[11] Injections were made in 0.25 or 0.5 cc. of cold blooded Ringer's.

Ergot. Dosages of Ergot Aseptic No. 29 (Parke, Davis and Co.) sufficient to produce marked paleness in black-adapted frogs evoked the opposite effect in pale winter flounders. One-fourth of 1 cc. caused darkening which lasted from 36 to 48 hours.

DISCUSSION

The role of the melanophore-dispersing principle in the pituitary of the flounder is still obscure. That the substance is present in the gland itself is definitely shown. Although the tests used are crude, it may be said that the summer flounder pituitary is not extremely low in this principle. More quantitative data will not be available until a series of comparative assays is carried out. Although this substance is present in the gland, it is not necessarily released into the circulation nor need it remain in an active form in the blood if it is released. Appropriate transfusion experiments and blood extractions have not yet been made. It is possible that that some inactivating enzyme is present to nullify the effects of even large amounts of the principle.

However, it would seem that if the melanophore-dispersing principle is really significant in producing the dark phase, some response should have been elicited by the injected preparations. Assuming that the melanophores of the winter flounder are relatively insensitive to the substance, it still seems that the highest dosages of intermedin should have evoked some response if the effectors react to it in the normal physiology of color change. It is difficult to believe that the fish's own pituitary is capable of supplying the circulation with more dispersing substance than would have reached the blood stream from the injections. However, although the dosages used were probably much greater than the fish could produce in its normal physiology it is possible that still higher doses could produce experimental darkening. There seem to remain, then, two lines of reasoning: 1) the melanophore system of the flounder is not stimulated by pituitary secretions which evoke darkening in other test animals or

2) some antagonistic substance or mechanism present in the injected fish is sufficiently strong to overcome relatively high doses of the active material.

In the first instance, it is perhaps as logical for this substance to be present yet play no part in color change as it is for it to be produced in the pituitaries of mammals which possess no chromatophores. Possibly it has some other function in the flounder as has already been suggested in mammals by O'Donovan and Collip ('38). It does not necessarily follow, however, that the substance could not also affect chromatophores.

In regard to the second alternative there is a very real possibility that the process of injecting the animal excites it to produce sufficient adrenalin-like substance to suppress any darkening reaction which might occur in response to the injected material. It is well known that a small amount of adrenalin injected simultaneously with intermedin will overcome the action of relatively large amounts of the latter. It is also clear that some excitement is associated with injection. This has been mentioned in the previous pages. Furthermore, it is possible that a trace of adrenalin-like substance too small to elicit any gross observable response might be sufficient to counteract any darkening effect of injected melanophore-dispersing substances. Yet, in a normal undisturbed fish, secretions from its own pituitary could be functional.

Since the pituitaries of winter flounders were not actually tested for melanophore-dispersing substance, it is possible that this species does not secrete the material. However, since these flounders are so similar to the summer flounder in general color behavior and since all pituitaries which have been tested have contained melanophore-dispersing substance, it is indeed unlikely that the winter flounder is any exception.

It is unfortunate that the hypophysectomized flounders lived only 2 days or less, not long enough to allow prolonged tests of color change, blinding responses, background responses, etc., in animals whose systems were unquestionably free from this secretion.

The negative results which were obtained, if reliable in animals hypophysectomized for so short a time, are comparable to those reported by Matthews ('33) in Fundulus. However, flounders are different in that denervated melanophores in faded areas do not darken to pituitary injection, in contrast to the findings in Fundulus by Kleinholz ('35).

Since the work of v. Frisch ('11), several investigators have observed fading subsequent to denervation and still later the ability of denervated melanophores to change color in harmony with the rest of the integument. Furthermore, the sudden paling of dark denervated areas has been associated with excitement and consequently the terms[12] 'psychic paling' and 'excitement pallor' have come into use. All of these responses must represent the action of supplementary non-nervous mechanisms which often become more obvious when nervous connections are severed. The psychic paling described by v. Frisch ('11) and Smith ('31 b) in Phoxinus, by Mills ('33) in Fundulus, and the excitement pallor reported by Bray ('18), Abramowitz ('36) and Osborn ('38) in the catfish are probably all similar to the excitement pallor described here for flatfishes. Smith ('31 b) definitely established the necessity of good circulation in areas showing this response. Several lines of evidence have contributed to show that the active paling substance is carried in the blood stream and its characteristic action so similar to adrenalin has naturally led to the descriptive term 'adrenalin-like.' However, the diffuse nature of the chromaffin tissue in teleosts makes its extirpation impossible and so the exact source of this substance is still an open question. Perhaps it is secreted at nerve terminals in the skin but if so, how is its production to be harmonized with the output of oil-soluble neurohumors as described by Parker? In fishes where both substances are presumably active, the problem of their production at nerve endings would indeed be complex.

---

[12] These terms are not limited to the responses of denervated areas. Sudden general paling responses following excitement have also been referred to in this way.

The paling produced by injections of serum from pale Gobius and Pleuronectes into dark specimens (Meyer, '31) was very likely due to the adrenalin-like material contained in the serum. However, if either of these species is anything like the winter flounder, it is surprising that she was able to produce darkening in pale fishes by injecting serum from black specimens. The very act of killing the fish preparatory to obtaining the serum might cause sufficient excitation to pale the fish before serum could be obtained. Just what the active darkening agent in her serum injections may have been is not known. The possibility of its being a pituitary substance is lessened but not disproved by the present experiments. Another darkening agent is suggested by the excitement responses of pale flounders. All three species exhibited temporary darkening when excited in the white-adapted condition, yet almost simultaneously, in the winter flounder, denervated areas paled. The excitement darkening of innervated melanophores is probably caused by nerves. Could the serum which produced darkening in Meyer's work have contained neurohumors secreted by these nerves?

The speed with which changes in shade occur in flounders together with the results of Pouchet's experiments had convinced investigators years ago that sympathetic nerves were highly significant in controlling this behavior. However, the ways in which sympathetic nerves are capable of producing the complex changes in shade and pattern have not been analyzed. Any mechanism which independently controls, in addition to the general shade of the entire surface, a configuration of local areas (spots) constant in position but variable in detailed shape and in shade intensity is necessarily complex. The fact that the general response and the spot response is at a given moment uniform in degree over the whole fish suggests that each is under the control of a separate set of fibers which are distributed over the body. Each of the sets would act independently but all the fibers of one set would carry identical impulses simultaneously. The question then arises as to how many sets of fibers control a definite shade. The general shade 'system' may range from extreme pale to extreme dark and theoretically consist of an infinite number of intermediate shades of gray. If we assume that every melanophore concerned in this reaction is doubly innervated with one concentrating fiber and one dispersing fiber, then a proper balance of impulses over both sets of nerves could produce the observed changes in general adaptation. Similarly, a double set of fibers to each melanophore of the 'system' of black spots and to each effector of the 'system' of white spots could produce the spotting responses as they occur. Colors would be produced by a similar innervation of erythrophores, xanthophores, etc. Such a plan would simply assume every chromatophore to be doubly innervated as has been suggested for certain other fishes. The unique difference would be in the independent control of the fibers to each 'system.' Although independently controlled, all the 'systems' would function in unison much of the time. Excitement would put the 'systems' out of unison and result in spots (black or white) appearing on a general surface of the opposite shade. Local independent control of any one spot probably does not exist because when one spot shows a response all others change correspondingly. The sand dab is perhaps more highly specialized as is evidenced by the fact that under proper stimulation the fins may spot without a similar response over the thicker parts of the body. However, the spots also appear on the thicker part when the stimulus is increased in intensity.

The foregoing hypothesis need not assume double innervation. A single set of fibers (either concentrating or dispersing) could function as effectively providing some counter influence (an inherent contraction or expansion of the chromatophore, a hormone, etc.) functioned to move the pigment in the direction opposite to that caused by the nerves. Experimental evidence has not yet established the existence of double innervation in the flounder. Furthermore, although experimental work has pointed to the role of the sympathetic nerves in color changes of these fishes, it is probable that parasympathetic fibers may play a part. This problem and the normal role of pituitary secretions in the natural color behavior of these animals still await more satisfactory interpretation. It is hoped that experiments, designed to elucidate some of these questions, which were terminated abruptly by the hurricane and flood, may be continued another season.

SUMMARY

1. Three species of flatfishes (Pseudopleuronectes americanus, Paralichthys dentatus and Lophopsetta maculata) adapt markedly to black or white illuminated backgrounds. The times necessary for these adjustments have been recorded. Repeated transfer from one background to the other results in acceleration in the rate of adaptation. Contrasting spots characteristic of each species exhibit specific background responses.

2. During the first few hours in total darkness, the behavior of the winter flounder and sand dab is influenced by previous exposure (white or black background). However, after a prolonged stay in darkness, an intermediate or darker homogeneous shade of brown is assumed which is apparently typical for both species. Generally speaking, the shade typical for total blindness was similar to that in total darkness. Blinded fishes are perhaps more homogeneous in shade (minimum of spots) than normal fishes in total darkness.

3. Denervation (bands or section of sympathetic chain) results in darkening which fades gradually but very slowly in white-adapted animals. After fading, the areas change in shade with the rest of the integument. Denervated areas in black-adapted fishes do not fade. In darkness, denervated bands do not fade and usually appear somewhat darker than the rest of the body. These species are not favorable for reactivation experiments. A limited number of operations did not produce dependable evidence favoring reactivation.

4. These flatfishes are very sensitive to exciting stimuli. Pronounced changes in shade occur in both innervated and denervated areas. Pallor and white spots appear in black-

adapted fishes but white-adapted fishes darken and produce black spots when excited. The reverse is true of the winter flounder whose spots disappear on excitement. In general the nature of the response is related to the intensity of the exciting stimulus. A marked excitement pallor occurs in denervated bands of the winter flounder which has been duplicated by injection of adrenalin. The adrenalin-like substance which causes excitement pallor is blood borne and is not an oil-soluble neurohumor. Its source is uncertain.

5. In the winter flounder it is possible to produce, in a previously denervated area so old as to contain only degenerated nerves, a dark band simply by cutting a fin ray. This band which appears dark in contrast to the surrounding denervated area paled by excitement, is probably due to circulatory congestion which serves to keep the adrenalin-like substance out of the new band. Since the nerves have degenerated it could not be a case of reactivation.

6. Adrenalin injected into any of these three species results in paling of innervated and denervated areas alike. The latter are more sensitive to small dosages. Denervating bands cut in fishes already paled by adrenalin do not appear dark until the adrenalin wears off.

7. Injections of minced or extracted pituitaries of summer flounders when tested in frogs and catfishes reveal that the melanophore-dispersing substance is present. Nevertheless, similar injections or dosages of concentrated intermedin or commercial pituitrin (Parke, Davis and Co.) failed to affect the shade of winter flounders. Furthermore, dosages of intermedin fifty times as great as were used in the test animals failed to evoke any color response in innervated or denervated areas in winter flounders.

8. In winter flounders injections of nicotine and ergot produced darkening.

9. The relatively rapid 'general background' and 'spotting' responses in these flounders are independently controlled by nerves. A theoretical discussion of the complexities of such a system is presented. These nervous reactions are supple-

mented by an 'adrenalin-like' substance to produce paling and 'excitement pallor' and may be suplemented by some non-nervous material to produce 'excitement darkening' in white-adapted fishes.

10. Despite the experimental results presented, a melanophore-dispersing substance from the flounder's own pituitary could assist natural darkening in undisturbed pale fishes.

LITERATURE CITED

ABOLIN, L. 1925 Beeinflussung des Fischfarbwechsels durch Chemikalien. I. Infundin- und Andrenalinwirkung auf die Melano- und Xanthrophoren der Elritze (Phoxinus laevis Ag.). Arch. mikrosk. Anat. u. Entw. mechan., Bd. 104, S. 667–698.

ABRAMOWITZ, A. A. 1936 Physiology of the melanophore system in the catfish, Ameiurus. Biol. Bull., vol. 71, pp. 259–281.

——— 1937 The role of the hypophyseal melanophore hormone in the chromatic physiology of Fundulus. Biol. Bull., vol. 73, pp. 134–142.

BRAY, A. W. L. 1918 The reactions of the melanophores of Ameiurus to light and to adrenalin. Proc. Nat. Acad. Sci., Washington, vol. 3, pp. 58–60.

FRIES, E. F. B. 1931 Color changes in Fundulus, with special consideration of the xanthophores. J. Exp. Zool., vol. 60, pp. 389–426.

VON FRISCH, K. 1911 Beitrage zur Physiologie der Pigmentzellen in der Fischhaut. Arch. ges. Physiol., Bd. 138, S. 319–387.

GIANFERRARI, L. 1922 Influenza dell-alimentazione con capsule serrenali, ipofisi ed epifisi sulla pigmentazione cutanea ed il ritmo respiratorio di Salmo Fario. Arch. Sci. Biol., vol. 3, pp. 39–52.

GIERSBERG, H. 1930 Der Farbwechsel der Fische. Zeitschr. vergl Physiol., Bd. 13, S. 258–279.

——— 1932 Der Einfluss der Hypophyse auf die farbigen Chromatophoren der Elritze. Zetischr. vergl. Physiol., Bd. 18, S. 369–378.

GILSON, A. S. 1926 The control of melanphore activity in Fundulus. J. Exp. Zool., vol. 45, pp. 457–468.

HEWER, H. R. 1925 Studies in colour changes in fish. I. The action of certain endocrine secretions in the minnow. Brit. J. Exp. Biol., vol. 3, pp. 123–140.

——— 1927 Studies in colour changes in fish. II. The analysis of the color patterns of the dab. III. The action of nicotine and adrenalin in the dab. IV. The action of caffeine in the dab, and a theory of the control of colour changes in fish. Phil. Trans. Roy. Soc. London, B, vol. 215, pp. 177–200.

KLEINHOLZ, L. H. 1935 The melanophore-dispersing principle in the hypophysis of Fundulus heteroclitus. Biol. Bull., vol. 69, pp. 379–390.

KROPP, B. 1929 The melanophore activator of the eye. Proc. Nat. Acad. Sci., Washington, vol. 15, pp. 693–694.

MAST, S. O. 1914 Changes in shade, color and pattern in fishes, and their bearing on the problems of adaptation and behavior, with special reference to the flounders, Paralichthys and Ancylopsetta. Bull. U. S. Bur. Fisheries, Washington, vol. 34, pp. 173–238.

MATSUSHITA, K. 1938 Studies on the color changes of the catfish, Parasilurus asotus (L.). Science reports of the Tôhoku Imperial Univ., Sendai, vol. 13, pp 171–200, Fourth Series.

MATTHEWS, S. S. 1933 Color changes in Fundulus after hypophysectomy. Biol. Bull., vol. 64, pp. 315–320.

MEYER, E. 1931 Versuche uber den Farbwechsel von Gobius und Pleuronectes. Zool. Jahrb., Abt. allg. Zool. u. Physiol, Bd. 49, S. 231–270.

MILLS, S. A. 1933 Evidence for a neurohumoral control of fish melanophores. J. Exp. Zool., vol. 64, pp. 245–255.

ODIORNE, J. M. 1933 The effects of the pituitary hormones on the melanophores of fishes. Proc. Nat. Acad. Sci., Washington, vol. 19, pp. 745–750.

——— 1937 Morphological color changes in fishes. J. Exp. Zool., vol. 76, pp. 441–465.

OSBORN, C. M. 1938 The role of the melanophore-dispersing principle of the pituitary in the color change of the catfish. J. Exp. Zool., vol. 79, pp. 309–331.

PARKER, G. H. 1934 a Color change of the catfish Ameiurus in relation to neurohumors. J. Exp. Zool., vol. 69, pp. 199–233.

——— 1934 b What part of the melanophore system in Fundulus is acted upon by adrenalin? J. Cell. and Comp. Physiol., vol. 5, pp. 311–318.

——— 1935 a An oil-soluble neurohumor in the catfish, Ameiurus. J. Exp. Biol., vol. 12, pp. 239–245.

——— 1935 b The chromatophoral neurohumors of the dogfish. J. Gen. Physiol., vol. 18, pp. 837–846.

——— 1936 The reactivation by cutting of severed melanophore nerves in the dogfish, Mustelus. Biol. Bull., vol. 71, pp. 255–258.

——— 1938 The color changes in lizards particularly in Phrynosoma. J. Exp. Biol., vol. 15, pp. 48–73.

POUCHET, M. G. 1872 Du role des nerfs dans les changements de coloration. J. Anat. et Physiol., vol. 8, pp. 71–74.

——— 1876 Les changements de coloration sous l'influence des nerfs. J. Anat. et Physiol., vol. 12, pp. 1–90; 113–165.

SCHARRER, E. 1928 Die Lichtempfindlichkeit blinder Elritzen (Untersuchungen uber das Zwischenhirn der Fische. I). Zeitschr. vergl. Physiol., Bd. 7, S. 1–38.

SMITH, D. C. 1931 a The action of certain autonomic drugs upon the pigmentary responses of Fundulus. J. Exp. Zool., vol. 58, pp. 423–453.

——— 1931 b The influence of humoral factors upon the melanophores of fishes, especially Phoxinus. Zeitschr. vergl. Physiol., Bd. 15, S. 613–636.

SPAETH, R. A. 1916 Evidence proving the melanophore to be a disguised type of smooth muscle cell. J. Exp. Zool., vol. 20, pp. 193–215.

——— 1918 Concerning a new method for the biological standardization of pituitary extract and other drugs. J. Pharmacol. Exp. Ther., vol. 11, pp. 209–219.

SUMNER, F. B. 1911 The adjustment of flatfishes to various backgrounds: A study of adaptive color change. J. Exp. Zool., vol. 10, pp. 409–505.

VEIL, C. 1937 Hypophysectomie et changement de couleur chez le poisson chat. Comptes Rendus, Acad. Sci., T. 124, pp. 111–113.

WYKES, U. 1937 The photic control of pigmentary responses in teleost fishes. J. Exp. Biol., vol. 14, pp. 79–86.

WYMAN, L. C. 1924 Blood and nerve as controlling agents in the movements of melanophores. J. Exp. Zool., vol. 39, pp. 73–132.

PLATES

PLATE 1

EXPLANATION OF FIGURES

1 A Undisturbed white-adapted winter flounder in which the sympathetic chain has been cut 30 minutes. Note the resultant darkened denervated area and the black spots posterior to the pectoral fin. One-third natural size.

1 B Same animal as in 1 A but mildly disturbed. Note the dark spots have disappeared.

2 Same animal as in 8 A. Photographed 6 minutes after electrical stimulation which caused the general mottling of the innervated area. Note that the previously dark denervated bands (fig. 8 A) have been paled by the exciting stimulus. One-quarter natural size.

3 A and 3 B Animals darkened by intramuscular injections of nicotine. The paler of the two received 0.1 cc. and the darker, 0.2 cc. of 1% solution. Both animals were originally white-adapted as in 5. One-fifth natural size.

4 Previously white-adapted animal which was blinded 20 hours before photographing. Note intermediate darkening. One-fifth natural size.

5 White-adapted animal which had remained on white 40 days. One-fifth natural size.

6 A and 6 B Two white-adapted fishes which have been on white for 22 days. Each has a new 10-minute-old denervated band (black). 6 B had been denervated posteriorly (sympathetic chain) 12 days before and 6 A possesses a nearly faded denervated band (22 days old) just posterior to the new band. One-sixth natural size.

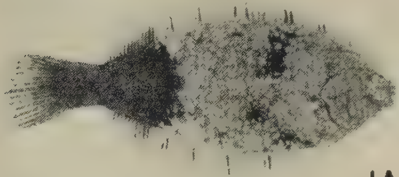
7 A and 7 B Same animals as in 6. 7 A possesses a newly denervated (6-minute-old) band just posterior to the faded one. Note that it has already darkened. A similar band was cut at the same time in the same relative position (in a previously denervated region in this case) in 7 B. Note that it has failed to darken.

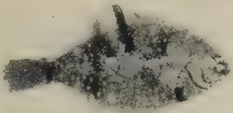
8 A and 8 B Same fishes as in 6 and 7. Black plate under fin shows whiteness is due to guanophores rather than transparency over a white background. Note partial fading of denervated bands.

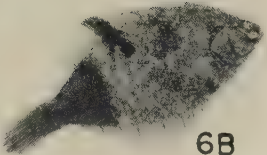
9 Black-adapted fish in which the denervated band (14 days old) has been paled by excitement. Photographed 12 minutes after electrical stimulation. One-fourth natural size.

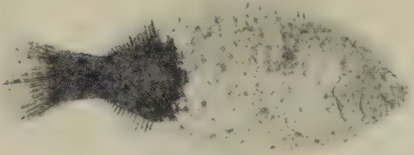
10 Same animal as in 9. Note narrow dark band along middle fin ray of previously denervated area. The new band was caused by cutting one ray 14 days subsequent to the original denervation. The new cut was made before the area was paled by excitement and was photographed 20 minutes after cutting.

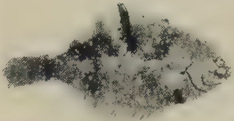
11 Black-adapted winter flounder which has been on a black background 4 days. One-fourth natural size.

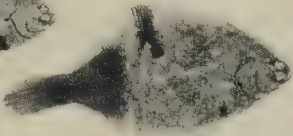

1A

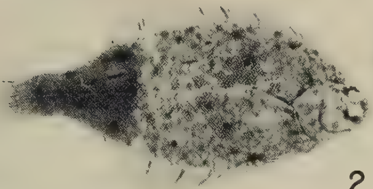

6A

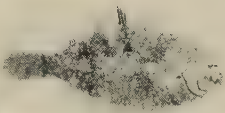

6B

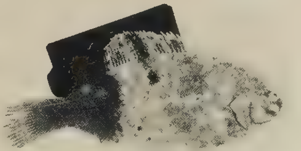

1B

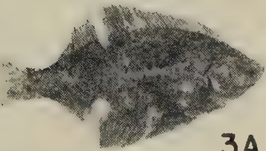

7A

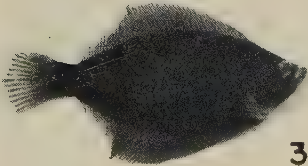

7B

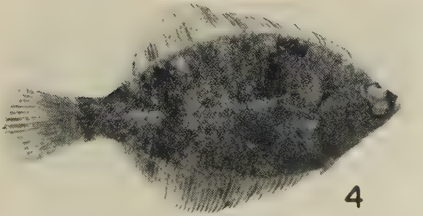

2


8A

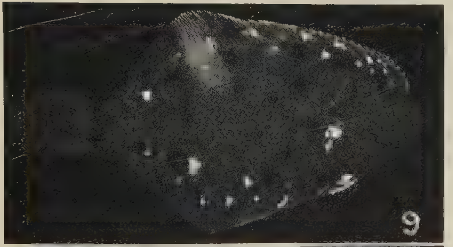

8B

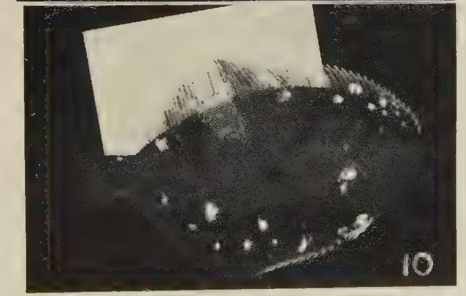

3A


3B


4

5


9


10

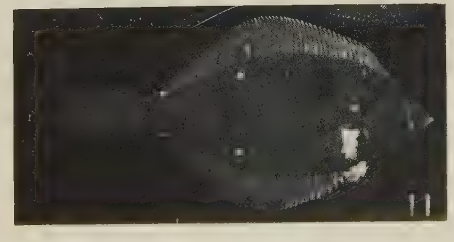

11

PLATE 2

EXPLANATION OF FIGURES

12 Black-adapted sand dab (Lophopsetta maculata) which had been on black for 3 days. Note small white spots. One-fifth natural size.

13 A Undisturbed white-adapted sand dab which had been on white for 6 days and in which a denervating band (black) had been cut 2 hours before photographing. One-quarter natural size.

13 B Same fish as in 13 A, slightly disturbed. Note dark spots on marginal fins and slight general darkening.

13 C Same fish as in 13 A, vigorously excited. Photographed 15 minutes after electrical stimulation. Note marked spotting of entire surface and general darkening sufficient to make denervated area (2½ hours old) almost indistinguishable.

13 D and 13 E Same fish as in 13 A after denervated band was cut. 13 D shows spotting and slight darkening to mild excitement. 13 E shows maximum spotting and pronounced general darkening of entire surface as a result of electrical stimulation.

14 A White-adapted sand dab in which the sympathetic chain was cut and a band was made 40 minutes before photographing. One-sixth natural size.

14 B Same fish as in 14 A. Partial paling of the denervated areas (5 hours old) 15 minutes after the intraperitoneal injection of 0.1 cc. of adrenalin. Note that the more central portions of the areas distal to the cuts pale least. This is probably due to circulatory congestion.

14 C Same fish as in 14 A. More complete paling of denervated areas photographed 90 minutes after the injection of adrenalin. Note the denervated band is whiter than any of the rest of the integument.

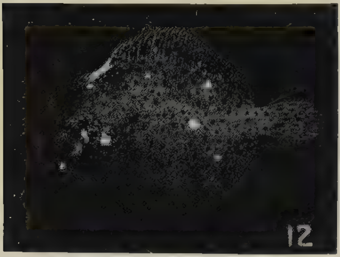
15 A Sympathetic chain in white-adapted sand dab cut 2 days before photograph was taken. Note that the darkened denervated region has faded slightly. Compare with 14 A. One-sixth natural size.

15 B Same animal as in 15 A. Photographed 7 days after denervating cut. Note degree of fading.

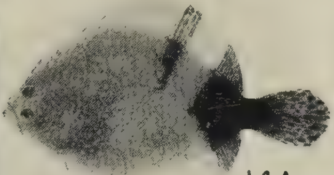
15 C Same animal as in 15 A. Photographed 7 days after operation and 2 minutes after electrical stimulation. Note the spotting reaction and general darkening of innervated integument but the absence of mottling on the homogeneously pale denervated portion.

16 A Black-adapted summer flounder (Paralichthys dentatus) which had been on black 40 days. Note the definite pattern of white spots (fish slightly disturbed). One-third natural size.

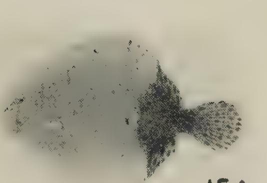
16 B Same fish as in 16 A. A denervating band including the third large white spot along the lower edge of the body musculature was cut 5 minutes previous to photographing. Note that denervation has annihilated the white spot by darkening it.



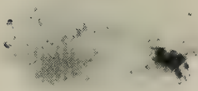
12



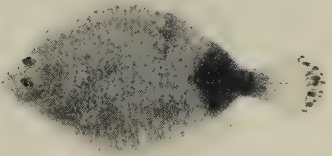
14A



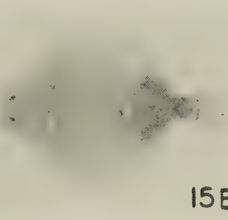
15A



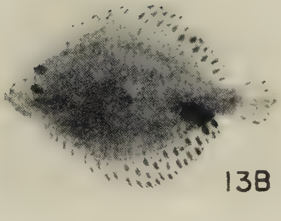
13A



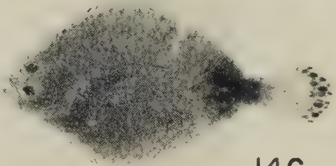
14B



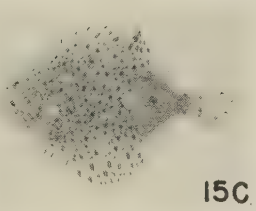
15B



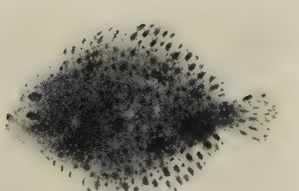
13B



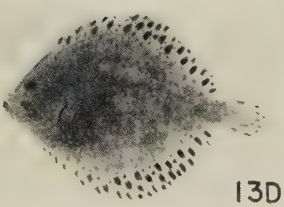
14C



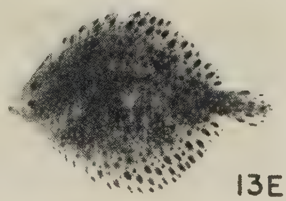
15C



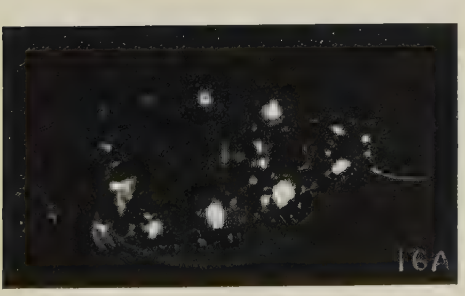
13C



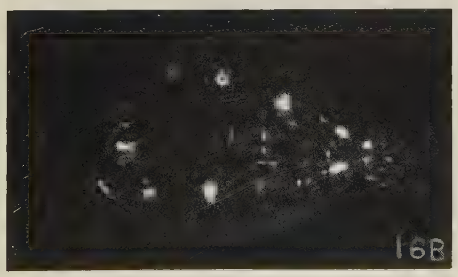
13D



13E



16A



16B

PLATE 3

EXPLANATION OF FIGURES

All the protographs in this plate are of the same summer flounder (Paralichthys dentatus) at about one-seventh natural size. They represent various degrees of background adaptation, excitement responses, and adrenalin effects in denervated areas.

17 A Adapted to white for 4 days. Sympathetic chain and a denervating band cut 4 hours previous to photographing. Note homogeneous blackness throughout denervated areas.

17 B One-tenth cubic centimeter of adrenalin was injected 4½ hours subsequent to denervating operations. Photographed 50 minutes after the injection. Note that the denervated areas have been partly paled by the adrenalin.

18 A The excitement response (white spotting). The stimulus was simply the sudden approach of the observer. The animal was previously homogeneously black as in 19 A.

18 B An excitement response of a white-adapted fish vigorously excited by very rough handling. Note the appearance of white and black spots and a general darkening of the whole surface. Before excitement, the animal was in the pale condition seen in 19 H.

19 A Homogeneously black-adapted, undisturbed. When photographed, it had been on black for 26 hours subsequent to the following history: taken from nature, 6 days on black, 8 days on white, then transferred to black where this photograph was made.

19 B Photographed 20 seconds after being transferred to white. Somewhat disturbed (spotting).

19 C Photographed 15 minutes later than 19 B. Somewhat disturbed again. Note the general shade is dark gray rather than black.

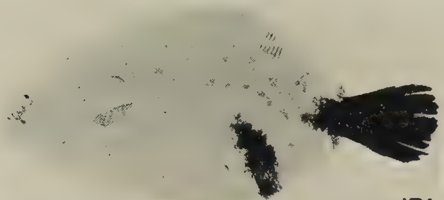
19 D Photographed 15 minutes after 19 C. Less disturbed than previously. Note that the general shade has paled enough to make the black spots distinguishable.

19 E Photographed 2¼ hours later than 19 D. Fish relatively undisturbed. Note homogeneous gray shade somewhat paler than intermediate.

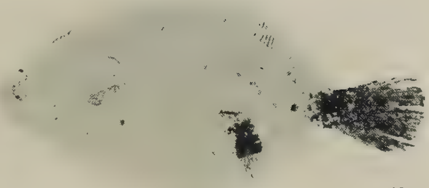
19 F Taken 2½ hours later than 19 E. Fish noticeably paler but also somewhat disturbed. Note that excitement now results in the appearance of black spots. Some spots even whiter than the general shade are also discernible.

19 G Thirty minutes later than 19 F. Almost completely white-adapted. Contrasting black spots elicited by an exciting visual stimulus. A hand was waved over the tank.

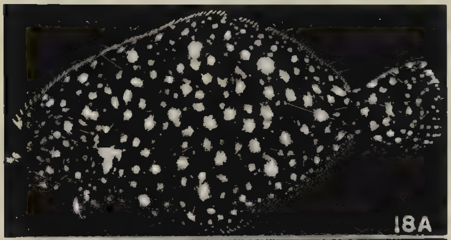
19 H Thirty-minutes later than 19 G. White-adapted fish relatively undisturbed. This complete adaptation was effected in about 6¼ hours. Note how this fish reacts to vigorous excitement in 18 B.



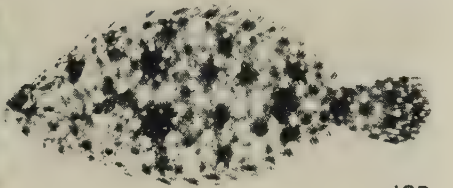
17A



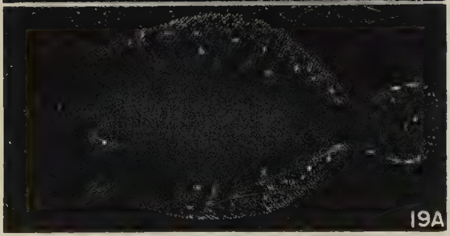
17B



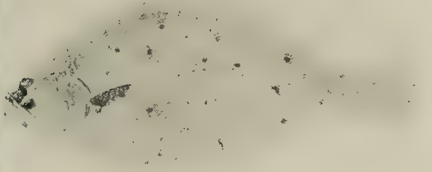
18A



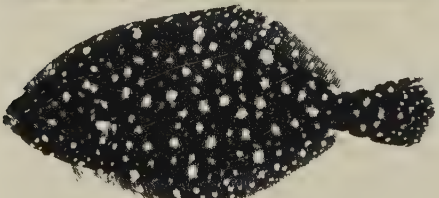
18B



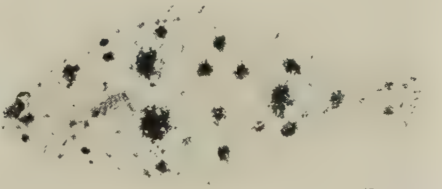
19A



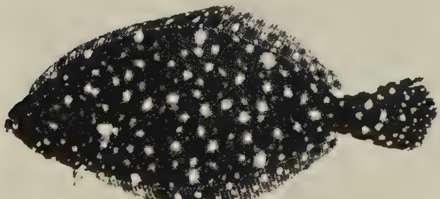
19H



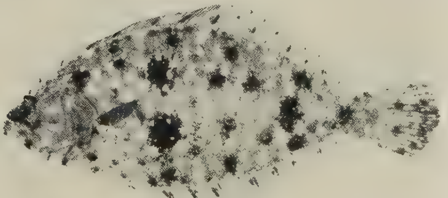
19B



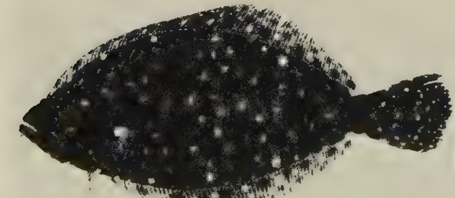
19G



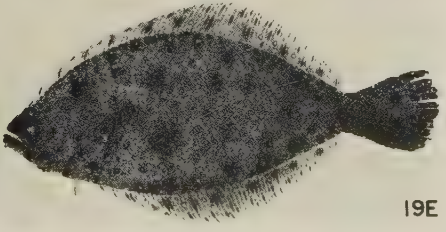
19C



19F



19D



19E

Contribution No. 20

Bull. Vol. VI, Art. 6

FURTHER OBSERVATIONS ON PENAEIDAE OF THE NORTHERN GULF OF MEXICO*

By Martin D. Burkenroad

Bingham Oceanographic Laboratory

CONTENTS

PAGES

INTRODUCTION 2

Relative abundance and bathymetric distribution of Penaeidae taken in 35 trawl-hauls on the continental shelf in the neighborhood of the Mississippi River.

SOLENOCERA Lucas 6

American species compared with related forms. Petasmal character distinguishing members of the genus with pterygostomian spine from those without.

S. NECOPINA n. sp. 7
S. ATLANTIDIS n. sp 10
S. VIOSCAI Burkenroad 13

Respiratory behaviour of living specimens compared with that of Penaeinae.

PENAEUS, Division 1 17

P. SETIFERUS (Linnaeus) 17

Redefined. Geographical distribution in relation to that of *P. schmitti* and to environmental factors. Occurrence of adults to a depth of 40 fathoms off the Mississippi. Evidence that copulation bears no close relation to time of oviposition. Evidence of survival after spawning and subsequent reappearance in the commercial catch. A new method (statolith-examination) for tracing the movements of this and other decapods.

PENAEUS, Division 2 26

Specific differentiation of the *P. brasiliensis* complex.

P. BRASILIENSIS Latreille 27
Redefined.
P. DUORARUM n. sp. 31
P. AZTECUS Ives 34

Redefined. Geographical distribution in relation to that of related species and to environmental factors; possibility that competition between species with identical tolerances but distinct optima of salinity may explain the peculiar differences in distribution between this and related forms. Adults limited off the Mississippi to 15–70 fathoms. Decrease in proportion of males to females with increasing depth, and relatively small maximum size in males, referred to longer life in females. Seasonal occurrence in a region (New Jersey) not suitable for an adult or permanent population. Probability that eggs of members of the genus do not float at the surface.

---

* Joint contribution from Woods Hole Oceanographic Institution (No. 203) and Bingham Oceanographic Laboratory.

PAGES
PARAPENAEUS Smith 53
Lateral armature of telson.
P. LONGIROSTRIS (Lucas) 53
Great numerical abundance and small maximum size in the area of the Mississippi.
TRACHYPENEUS Alcock 55
T. SIMILIS (Smith) 55
Distribution in relation to that of *T. constrictus* and to environmental factors.
T. CONSTRICTUS (Stimpson) 56
Coloration.
XIPHOPENEUS S. I. Smith 56
X. KRØYERI (Heller) 56
EUSICYONIA Stebbing 57
E. BREVIROSTRIS (Stimpson) 57
Coloration.
E. STIMPSONI (Bouvier) 57
E. DORSALIS (Kingsley) 58
CITATIONS 59

INTRODUCTION

As part of the work of an expedition aboard "Atlantis" in 1937, jointly sponsored by the Woods Hole Oceanographic Institution and the Bingham Oceanographic Foundation, and with equipment contributed by the Sears Foundation for Marine Research, a series of benthonic and pelagic trawlings was made in the northern Gulf of Mexico. Some systematic and ecological results of a study of the continental Penaeidae so obtained (exclusive of larval and post-larval forms) are offered in the present paper. A certain amount of material not derived from the 1937 expedition but needed for systematic or other comparisons is also included in the report.

The benthonic material obtained by the 1937 expedition was taken in two series of hauls with otter trawl and Blake dredge generally in combination with a one-foot stramin ring-net. The first series comprised 21 hauls beginning with St. 2812, 30° 08′ N, 88° 10′ W, March 20, and progressing in zig-zags southwestward to St. 2843, 27° 57′ N, 91° 43′ W, March 26. The second series comprised 14 hauls numbered as substations of St. 2853, made on April 9 and 10 within a quadrant approximately bounded by radii extending thirty miles southeast and northeast of the Pass a Loutre sea-buoy. Eight hauls altogether were made between 10 and 20 fathoms; eight between 21 and 40, thirteen between 41 and 70; and one at 100 fathoms. Of these thirty hauls, only two (one in 17, the other in 60–70 fathoms) failed to yield any peneids; the one at 100 fathoms yielded *Solenocera vioscai* and *Parapenaeus* only; in all but one of the twenty-seven remaining hauls one or two of three species of *Penaeus* were present, usually together with representatives of several other genera. Five hauls were also made between 130 and 500 fathoms, but these are not considered in detail in the present report; since although three of the hauls yielded peneids these are of species (*Benthesicymus bartletti, Plesiopenaeus edwardsianus, Hymenopenaeus robustus, H. debilis*) not found on the continental shelf. Three hauls on bottom at depths between 96 and 180 fathoms made in the northern Gulf during the 1935 expedition on "Atlantis" gave similar results in that of the peneids taken (*Hymenopenaeus debilis H. robustus, Solenocera necopina, Penaeopsis megalops, Parapenaeus longirostris*) only the last mentioned is known to occur in continental depths.

Bottom samples were procured by means of a small snapper at the stations of the second series; detailed examination of these samples has not yet been undertaken, but as might be expected the material collected consisted in all cases of a fine clayey deposit slightly variable in consistency and color but without any considerable proportion of coarse sand or shell. A number of trawls were lost in the course of the investigation, mostly toward or beyond the outer limits of the shelf, and it is possible that rough bottom of rock, shell or coral may have been present in some of these areas. Between 65 and 130 fathoms the trawlings frequently yielded enormous numbers of living heart-urchins, often little else. It may be observed that the area of trawling was more or less concentrated in the zone of high phytoplankton productivity described by Riley, 1937, p. 60; and that it lay entirely within the limits of greatest influence of the Mississippi.

It may be of interest to note that the deep-water catches of *Penaeus* gave off a powerful odor of iodoform such as characterizes the commercial catches of this genus from shallower depths with relatively much lesser frequency and intensity.

The maximum and minimum bottom temperatures and salinities in the areas of trawling (either obtained directly at the end of the haul or estimated from nearby hydrographic stations) were as follows: 10–20 fathoms, 19.2–20.7° C., 35.52–36.15°/oo; 21–40 fathoms, 16.2–20.3° C., 36.01–36.34°/oo; 41–70 fathoms, 16.2–18.2 °C., 36.07–36.33°/oo; 100 fathoms, 12.2–14.8° C., 35.91–36.08°oo/; 125–175 fathoms, 11.6–13.1° C., 35.44–36.04°/oo. The surface temperatures at the various trawling stations ranged between 15.8 and 21.9° C., the surface salinities between 04.29 and 36.10°/oo (mostly between 27.00 and 32.00°/oo). Surface temperatures below 18° C. were almost never found at salinities above 30°/oo, although at salinities below this value temperatures as high as 19.8° C. (as well as the lowest ones encountered) were recorded. To summarize the hydrographic observations, bottom temperatures diminish with depth; salinities increase with depth to *ca*: 70 fathoms and diminish thereafter, the inner limit of bottom salinity usually $\overset{=}{>}$ 36.00°/oo lying between 10 and 20 fathoms (or possibly a little deeper; *vide* Parr, 1935, p. 14), and the outer limit between 70 and 100 fathoms. Surface temperatures range only to 0.4° C. below and to 1.6° C. above the extremes to be found in 21–40 fathoms on bottom; surface salinities on the other hand are frequently far below any recorded from bottom; and consequently it would seem that shortly after the commencement of vernal warming, the bottom water at depths of less than 15 fathoms differs from that at moderately greater depths much more sharply in salinity than in temperature. Before the commencement of vernal warming, however, the bottom water at the shallowest depths might be expected to be colder than that at somewhat deeper levels. As pointed out by Professor Parr (in a personal communication) the freshening influence of the Mississippi outflow on the bottom waters may be expected to be relatively greater during the colder than in the warmer months.

The horizontal distribution of Penaeidae within the limits of investigation may be summarized as follows:

Five species (*Solenocera atlantidis, Penaeus duorarum, Trachypeneus constrictus, Eusicyonia brevirostris, E. stimpsoni*) of the nine taken at the three most easterly stations were absent from the twenty-one stations made around the mouth of the Mississippi between 88° 06′ W. and 89° 56′ W.; although the eastern stations were not particularly distinguished as regards temperature and salinity. Two of these five species (*Solenocera atlantidis* and *Eusicyonia brevirostris*) reappeared among catches from the six stations west of 89° 56′ W.; a third (*Trachypenaeus constrictus*) has been recorded by Burkenroad, 1934a, p. 102, from off Timbalier Bay (also, however, from directly off Pass a Loutre, though it is certainly infrequent here); a fourth (*P. duorarum*) finally is known from Vera Cruz (there being no critical records available for the enormous interval between Timbalier and Vera Cruz). Of the six species (*Solenocera vioscai, Penaeus setiferus, Penaeus aztecus, Parapenaeus longirostris, Trachypeneus similis, Xiphopeneus kroyeri*) taken at the stations between 88° 06′ W. and 89° 56′ W., it seems likely that several (particularly *P. setiferus* and *P. aztecus*) disappear from the Gulf of Mexico not far east of the region of investigation, perhaps in correlation with the diminishing influence of the Mississippi outflow (*cf.* Parr, 1935, fig. 10); the information available as to the northeastern Gulf is, however, extremely meager. To the west, critical records of *P. setiferus* and *P. aztecus* are available from Vera Cruz, so that the Gulf ranges of these species—like the influence of the great River—may perhaps extend much farther to west than to east of their presumed center of abundance in Louisiana.

The bathymetric distribution of the five species most abundant within the limits of investigation may be summarized as follows:

Solenocera vioscai was taken at 20 to 100 fathoms, in fourteen of the twenty-five hauls made between these limits; most frequently both as to individuals per fruitful catch and as to catches per total number of hauls within the given depth range at 20–40 fathoms. Mean frequency per fruitful catch about 11.

Penaeus setiferus was taken at 10 to 40 fathoms in seven of sixteen hauls between these limits, most frequently at 10–20 fathoms [this species ranges far inland into nearly fresh water only a few inches deep]. Mean frequency per catch about 130.

Penaeus aztecus was taken at 10 to 70 fathoms, in twenty-two of twenty-nine hauls between these limits. The species was taken most frequently as to individuals per catch in the shallower part of the area investigated, most frequently as to catches per total number of hauls in the deeper part, so that its abundance may evidently be said to be maintained nearly out to its deeper limit [this species ranges far inland into nearly fresh water only a few inches deep]. Mean frequency per catch about 11.5.

Parapenaeus longirostris was taken at 18 to 150 fathoms, in seventeen of twenty-seven hauls [including three made in 1935] made between these limits; most frequently at 30–70 fathoms. Mean frequency per catch about 96.

Trachypeneus similis was taken at 12 to 48 fathoms, in eleven of eighteen hauls between these limits, most frequently as to individuals per catch at 12–20 fathoms, most frequently as to catches per total number of efforts at 41–48 fathoms. Mean frequency per catch about 4.5.

SOLENOCERA Lucas

Prior to 1934, only one distinctively American form, *Solenocera agassizii* Faxon, was included among the fifteen species of the genus known until then. Consequently the discovery during the past three years that no less than six species of the genus occur in (and are limited to) America is a most unexpected and even disconcerting development. The American species form a rather homogeneous group distinguished as a whole from the other species with a pterygostomian spine (as far as is known) in the possession of a pair of strong, well-separated tooth-like projections on the anterior part of the fourteenth sternite of the females.

The other species with pterygostomian spine are the following: The Eastern Atlantic *S. membranacea* (Risso) [of which *S. distincta* DeHaan proves to be a specimen erroneously attributed to "Japon"] and the subspecifically distinct *S. m. africanus* Stebbing [an examination of the male type of which reveals that Stebbing's figure (suggested by Burkenroad, 1934a, p. 71, to be "either incorrect or represents a species other than the described female") is incorrect]; in which the anterior part of the cervical sulcus is bent posteroventrally without a recurved termination, and the lateral lobule of the distolateral lobe of the petasma is represented only by a minute vestige. The species, to be named in a future paper, represented by the female specimen from the Zanzibar area confused by Ramadan, 1938, p. 57, with what he terms "*S. rathbuni*" [= *S. lucasii* Rathbun (not Bate) a form lacking pterygostomian spine]; Ramadan's specimen (as distinguished from his figure) closely resembles *S. membranacea* but lacks a well-defined notch in the cervical carina and has a thelycum more like that of *S. novaezealandiae. S. comatus* Stebbing, the type of which lacks the genital sternites but which is extremely similar to the type of *S. novae-zealandiae* Borradaile (an adult female, not a juvenile male as erroneously believed by its author); in both of these the anterior part of the cervical sulcus curves forward as in the American species; but of the five rostral teeth three lie well in advance of the orbital margin and the anterior of the postorbital teeth is very widely separated from the epigastric.

In all of the species with pterygostomian spine of which the petasma has been examined (that is, in five of the American forms and in *S. membranacea*), the cincinnulated margin of this organ terminates far proximal to the distolateral lobe. It is therefore of considerable interest that in all members of the genus without pterygostomian spine, of which the petasma is known [comprising *S.*

melantho DeMan, *S. koelbeli* DeMan, *S. crassicornis* (H. M. E.) (and *S. sinensis* Yü), *S. hextii* W. M., *S. steindachneri* (Balss) [a peculiar species resembling *S. hextii* in most characters but with antennular flagella evidently like those of *S. annectans* Alcock; decidedly not a "*Haliporus*"], *S. pectinatus* (Bate) and what is evidently to be termed *S. rathbuni* Ramadan], the cincinnulated median margin of the organ reaches as high or nearly as high as does the distolateral lobe.

Solenocera necopina n. sp.

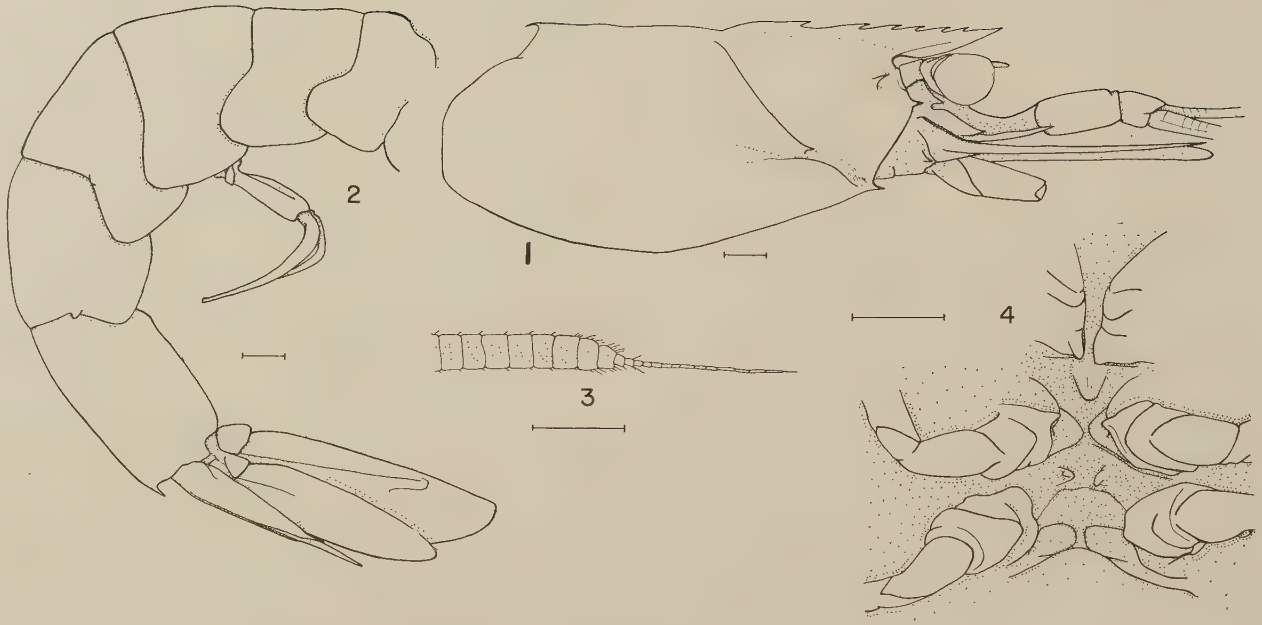
Figures 1, 2, 3, 4.

MATERIAL:

1 ♀. B. O. C. 225. HOLOTYPE. "Atlantis" St. 2377; N. 29° 16′, W. 87° 54′; March 24, 1935. Trawl, 125 fathoms.

Subadult. Carapace length 8.8 mm., rostrum, 2.8 mm.; telson, 4.7 mm.; total length about 34 mm.

DIAGNOSIS: Pterygostomian spine present, its margin joining that of the carapace dorsal to it by a gentle curve. Orbital angle marked but not acute or produced. Rostrum reaching a very little beyond the eyes; moderately slender; with a lower margin distinctly convex although tapering rather gently to the acute and slender tip; with a well-defined lateral ridge; armed above with six teeth of which two lie behind, one above the orbital margin. Distal rostral tooth a little farther from the rostral tip than from the antepenultimate tooth; posteriormost tooth four-fifths as far from the end of the postrostral carina as from the orbital margin and a little less than twice as far from the second tooth as this from the third. Postrostral carina not continued behind the level of the cervical sulcus. First through third pleonic terga uncarinated. Telson short, the length of its distal part beyond the large lateral spines not as great as the distance from tip of telson to tip of uropodal endopod. Antennular flagella moderately long, slender, a little more than twice as long as the carapace (minus the rostrum), at least thirty times as long as broad, with inferior flagellum about one-third broader than superior; ending in long slender tips, which in the case of the superior flagellum is about twice as long as in the inferior and about an eighth as long as the broad proximal part of the flagellum. Basal segment of antennular peduncle short; stylocerite as long as from its tip to the middle of the externodistal spine of the segment. Antennal scale relatively very long, extending beyond the antennular peduncle by about one-fifth its own length. Greatest breadth of the distal segment of the mandibular palp very little less than the length of the segment preceding it. Third maxillipede extends beyond antennal scale by about one-half its propodus. Carpus of third leg considerably longer than the more proximal joints together; third leg extends beyond antennal scale to about one-fifth of its carpus. Coxa of the fifth leg with a strong tooth on its anteromedian margin; coxa of the fourth leg only very little produced medially. Epipodites not bifurcated, the inferior ramus being indicated only by the nar-



Figures 1–4

Solenocera necopina, n. sp. **1.** Carapace and cephalic appendages; ♀ of car. 8.8 mm. (HOLOTYPE), × 5.5. **2.** Pleon with uropods; as 1, × 5.5. **3.** Superior antennular flagellum (distal part); as 1, × 12. **4.** Thelycum; as 1, × 12. Length of 1 mm. indicated at each drawing.

rowing of the blade beyond the point where the bifurcation originates in some species of the genus.

The teeth of the pair on the anterior part of the fourteenth sternite are long and slender and directed about vertically; their length is conspicuously greater than the interval separating them. The anterior part of the thirteenth sternite bears a high sharp ridge terminating abruptly just behind the posterior margin of the twelfth sternite.

According to notes on the freshly-captured specimen (Burkenroad, 1936a, p. 123) the color is pale orange-red over-all, without conspicuous banding.

REMARKS: *S. necopina* is known only from a single specimen taken at the edge of the continental shelf in the northern Gulf of Mexico, which was erroneously described by Burkenroad, 1936, p. 122, as a young individual of *S. vioscai* Burkenroad. Examination of the series of juveniles of *S. vioscai* recently captured in the Gulf of Mexico and reported in a subsequent paragraph indicates that critical characters of this species are unchanged at sizes much smaller than that of *S. necopina.* In particular, the minimum number of rostral teeth in *S. vioscai* of all sizes is eight; and except in the youngest post-mysis instars, of carapace length less than 3 mm., the orbital angle is produced and tooth-like; the post-rostral carina is clearly continued nearly to the posterior margin of the carapace; the posterior part of the third pleonic tergite is distinctly carinated; the telson extends to within much less than half the length of its terminal part toward the tip of the uropodal endopod; the antennular stylocerite is not so long as the distance between its tip and the base of the spine of the anterolateral corner of the basal segment of the peduncle; the antennal scale extends little (rarely to as much as one-tenth its own length) beyond the tip of the antennular peduncle; and there are numerous other minor differences. Finally, at sizes equivalent to that of *S. necopina*, the females of *S. vioscai* are obviously juvenile, and the paired teeth of their fourteenth sternite are hardly perceptible swellings.

In reduced rostral armature and absence of dorsal carina behind the cervical sulcus of the carapace and on the third pleonic tergite, *S. necopina* displays considerable resemblance to *S. atlantidis* n. sp. to be described below; but it differs from this species (and from the two related Pacific American forms *S. mutator* and *S. florea* Burkenroad, 1938) and resembles S. *vioscai* (and the Pacific American *S. agassizii* Faxon, Burkenroad, 1936 and 1938), in the gently curved juncture of the frontal margin of the carapace with the pterygostomian spine. *S. necopina* differs from *S. atlantidis* (and indeed from all of the American species) in the obtuseness of its orbital angle [in which feature it resembles the Indo-Pacific *S. comatus*, and differs from *S. membranacea* and from the species represented by the Zanzibar female erroneously attributed by Ramadan, 1938, to his "*S. rathbuni*"] and in the great length of its antennal scale. Its thelycum differs from that of *S. atlantidis* in the well-defined ridge of the anterior part of the thirteenth sternite. Like the other Atlantic American species of the genus, *S. necopina* differs from all of the Pacific American forms in the shallower bifurcation of its epipodites.

Solenocera atlantidis n. sp.

Figures 5, 6, 7, 8, 9, 10.

MATERIAL:

163 ♂, 206 ♀. *B. O. C. 238.* HOLOTYPE (♀, *B. O. C. 239*) and COTYPES. "Atlantis" St. 2813; March 20, 1937. Trawl, 19 fathoms.

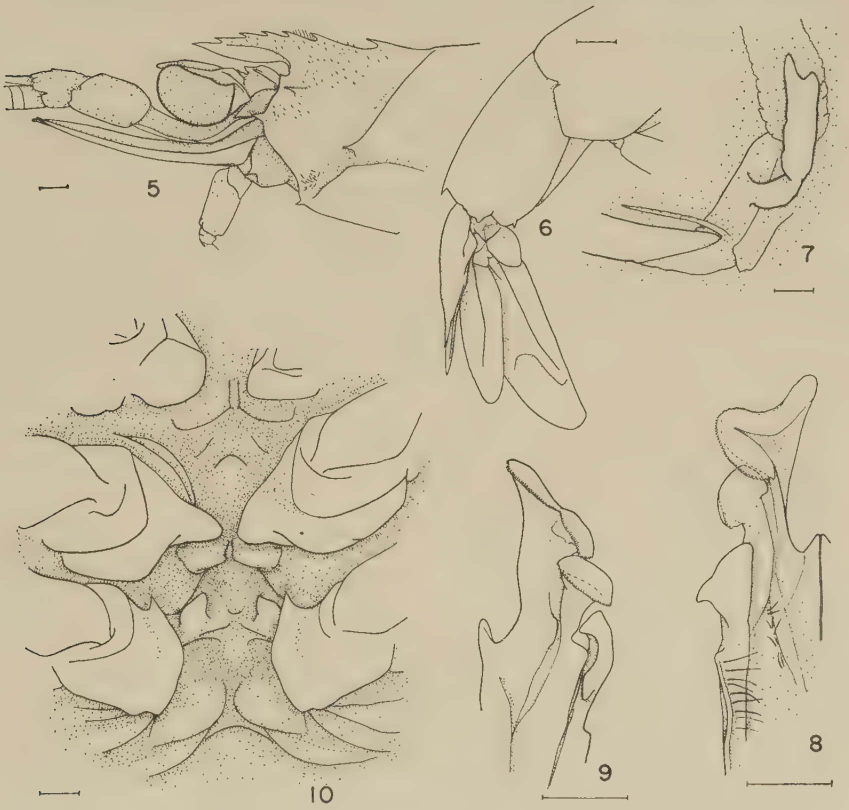
1 adolescent. *B. O. C.* "Atlantis" St. 2830; March 23, 1937. One-foot stramin net, 20 fathoms.

Females ranging from carapace 15.3 mm., total length about 55.5 mm. (rostrum 4.1 mm., telson 7 mm.), to carapace 5.7 mm., total length 21 mm. Males ranging from carapace 8.9 mm., total length 37 mm. (rostrum, 2.6 mm., telson 4.7 mm.) to carapace 5 mm., total length 18.5 mm. In only one single male, the smallest one, are the petasmal endopods disunited. Nearly all of the females, of all sizes, display well-ripened ovaries (most advanced in some of the larger specimens), although none is impregnated and none appears to have already spawned. Practically the entire catch at Station 2813, therefore, including individuals down to lengths of 25 mm. or less, seems to consist of sexually mature adults.

The minute adolescent specimen of St. 2830 has a carapace length of about 2.2 mm., total about 8 mm.

DIAGNOSIS: Pterygostomian spine meeting the frontal margin of the carapace at a right angle; in a few variant individuals the spine is doubled. Orbital angle acute and more or less tooth-like though often not greatly produced. Rostrum not reaching so far as do the eyes, moderately deep, its convex lower margin curving upward distally to form a slender but saber-shaped tip; rostrum with a distinct lateral ridge; armed above with five to seven, usually six, teeth of which two lie behind, one above the orbital margin. Interval between the distal rostral tooth and the rostral tip variable, usually equal to interval between distal and penultimate or antepenultimate teeth; posteriormost tooth from three-fifths to four-fifths as far from the end of the postrostral carina as from the orbital margin; about twice or a little more as far from the preceding tooth as this from the third tooth. Postrostral carina not continued behind the crossing of the cervical sulcus. First through third pleonic terga uncarinated. Telson short and broad, but owing to the extreme shortness of the uropods, the length of its distal part beyond the large lateral spines is greater or considerably greater than the distance from tip of telson to tip of uropodal endopod. Habitus stout.

Antennular flagella relatively rather short and slender, modally about one and one-half times as long as the carapace; at least thirty times as long as broad; inferior flagellum about two-fifths broader than superior. The slender flagellar tips are less than one-thirteenth as long as the broad, hollowed proximal portions. Antennal scale extending beyond the antennular peduncle for about one-fifteenth or less (rarely, as much as one-tenth) of its own length. Mandibular palp relatively very broad; the breadth of its distal exceeding the length of its proximal segment. Third maxillipede extends beyond the antennal scale by about one-third of its propodus. Carpus of third leg somewhat longer than more proximal joints combined; third leg extends beyond antennal scale to about one-seventh of its carpus. Coxa of fifth leg with a strong tooth on its anteromedian margin, in both sexes; coxa of the fourth leg of the female somewhat



Figures 5–10

Solenocera atlantidis, n. sp. **5.** Carapace and cephalic appendages; ♂ of car. 8 mm. (COTYPE), × 3.8. **6.** Pleon (posterior part) with uropods; as **5**, × 5. **7.** Epipodite (of left third cheliped); as **5**, × 5. **8.** Petasma (right endopod, posterior view of distal part); as 5, × 11. **9.** Petasma (right endopod, lateral view of distal part; as 5, × 11. **10.** Thelycum; ♀ of car. 14.5 mm. (COTYPE), × 5. Length of 1 mm. indicated at each drawing.

produced medially but not enough to meet its fellow of the opposite side. Epipodites usually mitten-shaped; sometimes quite distinctly bifurcate but the thumb or inferior branch never exceeds one-third of the length of the proximal part of the blade, excluding the peduncle.

Teeth of the pair on the anterior part of the fourteenth sternite of the female moderately long but usually separated by an interspace greater than their length, sometimes, however, closely approximated. Posterior outline of thirteenth sternite shallowly emarginate; anterior part of thirteenth sternite somewhat swollen and setose with a small central elevation, but no longitudinal carina.

Posterior margin of the fourteenth sternite of the male narrowly incised medially. Distoventral lobe of the petasma of the male without a free projection from its tip which does not reach so high as the distomedian lobe; the setose ridge along the proximal part of the lateral edge of the lobe extends well beyond the middle of the margin. The lateral lobule of the distolateral lobe is strongly developed. The median lobule of the distolateral lobe is large and of a subtriangular, or bilobed, shape. The anterior face of the distolateral lobe bears a very low, arcuate lamellate projection.

According to notes on the freshly-captured specimens, the pigmentation is orange-red; the color is most concentrated as bands across the posterior parts of the pleonic tergites.

REMARKS: Three hundred and sixty-nine mature specimens of *Solenocera atlantidis* were taken in one single haul, yet only one, a very young specimen was found thereafter in many hauls over apparently similar bottoms in the same general region. In this respect the economy of the present species seems similar to and as puzzling as that of *Hymenopenaeus debilis*, of which an enormous catch was made by "Atlantis" off the Mississippi in 1935, but which occurred, and then sparingly, in only one of several hauls at appropriate depths in 1937.

Solenocera atlantidis is very nearly related to the Pacific American *S. mutator* and *S. florea* Burkenroad, 1938, from which it is distinguished by the less developed bifurcation of its epipodites. In sculpture of posterior pereionic sternites *S. atlantidis* rather resembles *S. florea*. In petasma *S. atlantidis* (although somewhat like *S. florea* in that the body of the distoventral lobe does not rise above the distomedian lobe, and the setose ridge on the lateral edge of the distoventral lobe extends well past the middle of the margin) differs very conspicuously from the other American species of the genus and resembles all of the non-American species of which the petasma is known by the lack of a free projection at the tip of the distoventral lobe. The lamellate projection of the anterior face of the distolateral lobe is much less developed than in *S. florea* and *S. mutator*, and the median lobule of the same lobe has a quite distinctive form. *S. atlantidis* may be instantly distinguished from small individuals of *S. vioscai* by its less numerous rostral teeth, the right angle made by the juncture of its pterygostomian spine with the frontal margin, the lack of carination on the posterior part of the dorsum of its carapace and third pleonic segment and its quite different sexual structures.

Although the very young specimen of *S. atlantidis* taken at St. 2830 differs from the adults in a number of features (the pleurobranchs and prosartema being not yet fully matured, etc.), the characteristic form of pterygostomian spine and of rostral armature are clearly recognizable.

It seems probable that the smallest of the three Venezuelan females reported as *Solenocera siphonocera* by Smith, 1886, p. 186, and attributed to *S. vioscai* by Burkenroad, 1934a, p. 65, is actually distinct from the other two individuals of this lot; but whether it may be referable to *S. atlantidus* is not certain.

Solenocera vioscai Burkenroad

Figures 12, 13, 14, 15

S. vioscai, Burkenroad, 1934a, p. 65, part; 1938a.
S. siphonocera, Smith, 1886, p. 186, part.
NOT *S. vioscai*, Burkenroad, 1936a, p. 122.

MATERIAL:

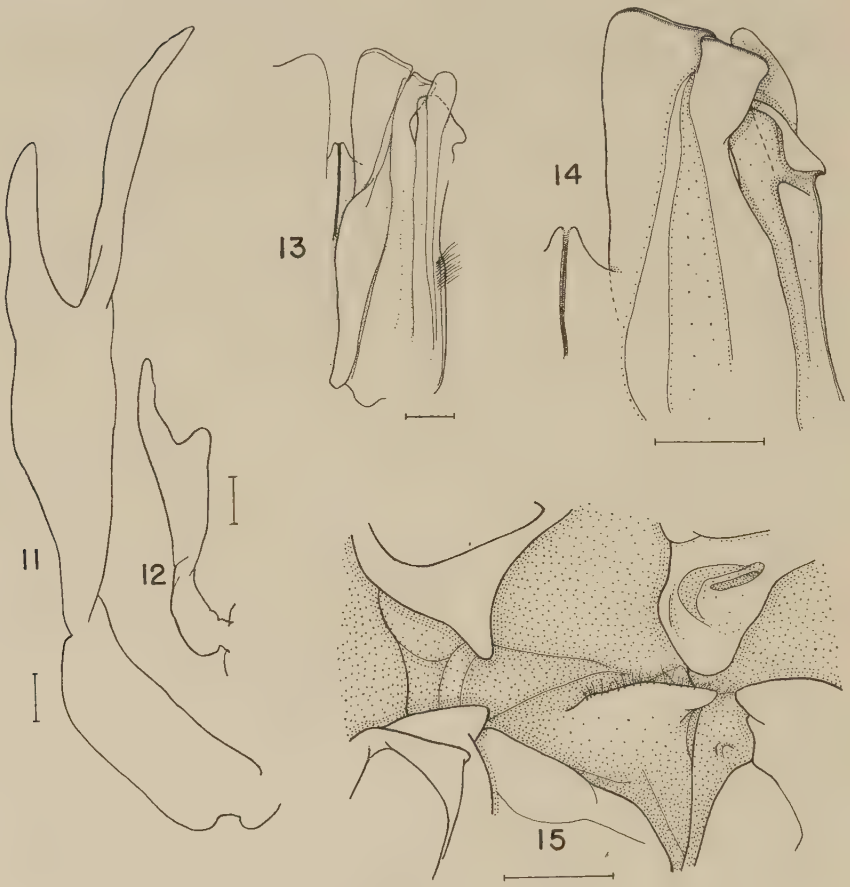
65 ♂, 63 ♀, 13 adolescent. *B. O. C. 241* to *254*. "Atlantis" St. 2814, 2838, 2840, 2843, 2853 No. 3, 5, 6, 7, 8, 10, 11, 12, 13, 14; March 21–April 10, 1937. 20–103 fathoms.

Females ranging from carapace 29 mm., total length about 118 mm., to carapace 6 mm., total length about 26 mm. Males ranging from carapace 18 mm., total length about 82 mm., to carapace 5.2 mm., total length about 21 mm. The samples are heterogeneous as to size, large and small specimens being taken in the same haul; small outnumber large specimens in most of the hauls. In males of carapace length less than 10–8.5 mm., the petasmal endopods are unjoined and poorly developed; above 10 mm. the petasma is of adult form. In some of the females of carapace length greater than 19 mm. the ovaries are filled with ripening eggs; in other large specimens, and in the smaller ones, the ovary is little advanced. None of the females are impregnated.

The adolescent specimens range in carapace length from 2.1 mm. to 2.7 mm.; greatest total length about 10 mm. The largest appears to be no more than a very few molts from the mysis stage.

REMARKS: *Solenocera vioscai* has previously been known only from four subadult to adult females, two taken off Venezuela, two off Louisiana; since two small females with only six rostral teeth, previously identified with the larger specimens (in the erroneous belief that they represented the young form) by Burkenroad (1934a; 1936), are now discovered to be referable to other species than the present one.

Since the other two species of the northern Gulf of Mexico, *Solenocera necopina* and *S. atlantidis*, have each been taken on only a few occasions, no very sure



Figures 11–15

Solenocera agassizii Faxon. **11.** Epipodite (of right third cheliped); ♀ of car. 40 mm. ("Albatross" St. 3391, Un. Zool. Mus Copenhagen), × 6.

S. vioscai Burkenroad. **12.** Epipodite (of right third cheliped); ♀ of car. 19 mm. (Louisiana, *B. O. C.* No. 253), × 6. **13.** Petasma (left endopod, posterior view); ♂ of car. 14 mm. (Louisiana, *B. O. C.* No 253). × 6.5. **14.** Petasma (right endopod, anterior view of distal part); as 13, × 14. **15.** Thelycum (pereionic sternite XIII, ventrolateral view); as 12, × 14. Length of 1 mm. indicated at each drawing.

conclusions as to differences in their geographical and bathymetric distribution can be drawn; but it seems worth note that the former was found beyond the greatest depth, the latter at the shallow extreme of the range [(15) 20–100 fathoms] occupied by *S. vioscai;* that *S. atlantidis* occurred to east and to west of the Mississippi Delta but not directly off the Passes where *S. vioscai* was very abundant; and that *S. vioscai* was not taken at either of the two stations where *S. atlantidis* occurred.

According to the present extensive material, the amount of variation in characters of *S. vioscai* of systematic importance is rather slight. Form of pterygostomian tooth and number of rostral teeth are characteristic even in the minute adolescents, although the postcervical portion of the postrostral carina and the carina of the third pleonic tergum are absent in these very small specimens. In the larger specimens, juvenile to adult, the number of rostral teeth ranges from 8 to 10, usually 9, at all sizes; position of posteriormost (epigastric tooth) is constantly twice as far from the orbit as from the crossing of the cervical sulcus. Rostrum occasionally does not exceed the eyes; and its lower margin is in a few individuals somewhat convex. The lateral teeth of the telson are generally much better developed than is shown in the figure of the type (Burkenroad, 1934a). The long and slender antennular flagella (two and one-third to three times as long as the carapace) terminate in a slender filament about one twenty-fifth as long as the expanded portion. Antennal scale never overtops the antennular peduncle by more than one-tenth its own length, usually much less. Epipodites are usually no more than mitten-shaped, hardly to be termed bifurcate. Coxa of the fifth leg of the females is in some specimens completely unarmed (as also, it now appears, in some specimens of *S. agassizii*), in others bears a minute tooth on its anteromedian edge. The high, sharp median ridge of the anterior part of the thirteenth sternite, terminating at its anterior end as an overhanging tooth closely appressed to the posterior margin of the twelfth sternite, is conspicuous in females whether juvenile or adult.

The petasma of *S. vioscai*, which has not been previously described, resembles that of *S. agassizii* Faxon (Burkenroad, 1936) and differs from that of *S. atlantidis*, *S. florea*, and *S. mutator* in its complete lack of a lamellate projection from the anterior face of the median lobule of the distolateral lobe; and also in that the body of the distoventral lobe considerably overtops the distomedian lobe. The petasma differs from that of *S. agassizii* particularly in the undivided and unproduced form of the median lobule of the distolateral lobe, which hardly overtops the lateral lobule; and also in that the setose ridge along the proximal part of the lateral edge of the petasma ends far proximal to the middle of the margin instead of extending much farther distally as in *S. agassizii*.

According to notes on a large living female, the coloration of *S. vioscai* is in general pale orange interspersed with many translucent areas; the pigment is particularly concentrated on rostrum and antennules, and as bands across the posterior parts of the pleonic terga. There are patches of opaque white on the outer sides of the legs and pleopods, on the uropods, and at the posterior margins of the fourth and fifth pleonic segments. The ovary is creamy orange.

NATURAL HISTORY: On two occasions, at Stations 2814 and 2838, large females of *S. vioscai* came up alive in the trawl and were maintained under observation in aquaria, in one case for more than twelve hours. One of the specimens in particular seemed to be in good condition, and both were alive and vigorous when cast into preservative at the end of the periods of examination. The specimens moved with great slowness and deliberation except when strongly stimulated, when they were capable of jerking rapidly backward; they showed no tendency to swim. The stronger specimen drew itself down into the mud at bottom of its receptacle, not so much burrowing as burying the posterior part of its body in the soft silt; its attitude was usually a strongly reflexed one so that the antennular flagella projected from the mud at an angle of about 45°. In both cases, respiratory water was observed to enter the branchial chamber only from its anterior end, whether the animals were buried in silt or not. While buried in the silt, respiratory water was certainly obtained largely from the opening at tip of the conduit formed by the apposition of the antennular flagella, since the current entering this opening was very perceptible. When the animal was at the surface of the mud the amount of inflow leakage around the anterior margin of the carapace or along the antennular peduncle was seen to be variable, but was often practically non-existent. At intervals the second maxillipedes were lowered and the mud which had settled above them was cleared away by a vigorous anteriorly-directed jet of water.

Although the opinion that the antennular flagella of *Solenocera* form a respiratory conduit (as opposed to the occasional view that the tube exists for the protection of the inner flagella) has been rather generally held, the usual conception appears to have been that the antennular tube is an efferent channel (*cf.* Stebbing, 1893, p. 218). The contrary suggestion of Burkenroad (1934a, pp. 66, 138) that the conduit is an afferent one is confirmed by the present observations, as is also the suggestion previously made by Burkenroad on morphological grounds (*l. c.*) of a sedentary, burrowing habit in which the normal attitude is a strongly reflexed one.

While the habit of partial or complete burial occurs in many littoral Penaeinae which at other times, as by night, are active and may even enter the nekton (*cf.* Wheeler, 1937), and while these forms usually take up a more or less reflexed attitude (to the extent permitted by their unmodified first pleonic tergite) when buried, the direction of branchial flow seems in them always to be the usual one from posterior to anterior, and the efferent current is discharged at the tip of an unprolonged conduit formed by the antennular peduncles and antennal scales. As the animals (for example, *Penaeopsis*) frequently penetrate so deeply into the substratum as to bring the end of the conduit far below the surface, this arrangement for discharge seems perhaps of particular value in removing the breathed water as far as possible from the region of intake under conditions where movement of the surrounding medium is impeded. The occurrence in *Solenocera* of a different means of breathing from that successful in other peneids of burrowing habit may perhaps be related to the consistency of the substratum inhabited;

thus, simple filtration along the edges of the carapace might perfectly protect the gill surfaces from clogging in a *Metapenaeopsis* buried in sandy mud or sand at Bermuda, but be completely ineffective in the extremely fine silts off the Mississippi Delta. It would be of great interest to know whether *Solenocera* is limited to oozy bottoms, and whether species of other genera (as *Penaeus aztecus*, *Trachypeneus similis*) found in such areas are contrasted in habit (as regards burrowing) to their relatives (*P. duorarum*, *T. constrictus*) of grainy bottoms.

PENAEUS Fabr.

Division I

Penaeus, Division I, Burkenroad, 1934a, p. 74.

Penaeus setiferus (Linn.), restricted

? *Cancer setiferus*, part, Linaeus, 1767, p. 1054.
? *Penaeus orbignyanus*, Latreille, 1817, p. 154.
Penaeus fluviatilis, Say, 1817, p. 236.
Penaeus setiferus, H. Milne Edwards, 1837, p. 414; auct., part.
Penaeus gracilirostris,[1] Thallwitz, 1891; DeMan, 1911, p. 100.
Penaeus setiferus, Weymouth, Lindner and Anderson, 1933, p. 23, part; Burkenroad, 1934a, p. 77; 1936, p. 316.
Penaeus brasiliensis aztecus, part, Ives, 1891, p. 190.
NOT *Penaeus setiferus*, Heller, 1868, p. 121.

Material:

1 ♂. NEOTYPE. *B. O. C. 237*. (From *B. O. C. 86*, 29 ♂, 24 ♀), off Matanzas Inlet, Florida; April 2, 1934. 8–10 fathoms, ottertrawl. Mr. M. B. Bishop.
221 ♂, 376 ♀. *B. O. C. 321* to *327*. "Atlantis" St. 2812, 2820, 2822, 2828, 2839, 3853 No. 12; March 20–April 10, 1937. 10–39 fathoms.
19 ♂, 19 ♀. *B. O. C. 328* to *330*. Pensacola Bay, Florida; March 11, 13, and 16, 1935. 5 fathoms.
1 ♂, 1 ♀. *B. O. C. 331*. Gulf of Mexico off Pensacola; March 23, 1935. 5 fathoms.

Neotype, carapace length 38 mm., total about 165 mm. "Atlantis" 1937 material, carapace length of males from 25.5 mm. to 42 mm.; of females from 27 mm. to 48.5 mm. Males from Pensacola, carapace 23 mm. to 29 mm. except for the largest, of 34 mm.; females 21 mm. to 28.5 mm. except for the largest, of 32.5 mm. Joining of the petasmata occurs in males between 25 and 26.5 mm.

Remarks: In 1934a, p. 84, the possibility that *Penaeus setiferus* auct. might include more than one species was briefly suggested by Burkenroad, who in

---

[1] An examination of the type of *P. gracilirostris*, made possible by the kindness of Dr. H. Kummerloewe of the Dresden Museum, leaves no room for doubt that the reported derivation of this "unique" specimen ("North Celebes") is entirely erroneous.

1936b, p. 315, separated a southern species (*P. schmitti*) from a northern one for which the name *P. setiferus* (Linn.) was employed without formal redefinition. The history of the Linnean name is the following:

The habitat of *Cancer setiferus* is stated by Linné, 1767, p. 1054, to be "in Indiis"; a reference is made to the "*Astacus fluviatilis*" ["d'Amerique"] of Seba, 1758. In the non-Linnaean thirteenth edition of "Systema Naturae," 1788, the habitat of *Cancer setiferus* is described as southern America and India. According to Mr. S. Savage of the Linnaean Society, nothing is known in London of the material upon which *C. setiferus* was based [unless it is included among some unlabelled and miscellaneous arthropodan fragments not certainly of Linnean origin]; and according to Dr. G. Jagersten, the type is not preserved at Uppsala. It seems not impossible that the Linnean imputation of American habitat to *C. setiferus* was derived from Seba, and that the type was a specimen from the East Indies which somewhat resembled Seba's plate; however, the name has subsequently been employed exclusively for Atlantic American material.

Herbst, 1796, describes the habitat of *Cancer* (*Gammarellus*) *setiferus* as America.

Say, 1817, in describing a species of the Fabrician genus *Penaeus*, which he regards as identical with Seba's *Astacus fluviatilis*, overlooks or ignores the Linnean reference to Seba's prawn and terms his material *Penaeus fluviatilis*. Say describes the species as abundant "in the estuaries of the southern states and Florida." H. Milne Edwards, 1837, synonymizes *P. fluviatilis* with the Linnean species and presumably derives from Say the statement that *Penaeus setiferus* inhabits the mouths of the rivers of Florida [since according to Bate, 1881, the surviving Edwardsian specimen is labelled "Guadaloupe" (a most indefinite provenance perhaps referring to San Antonio Bay, Texas, at the mouth of the Guadaloupe River)]. *P. setiferus* is employed by DeKay, 1844, and by Gibbes, 1850, for material from the United States. In 1858, deSaussure applies the Linnean name for the first time to material from defined localities (Cuba and Tampico) outside of the present limits of the United States; it is not impossible that both of the two forms now recognized inhabit Cuba, but material from Tampico was probably of the northern species.

In 1865, the name *P. setiferus* was used for the first time, by Heller, for material from (Rio de Janeiro) within the definitely known range of *P. schmitti;* and a reëxamination of the single specimen of this group taken at Rio by the "Novara" shows it to be of *P. schmitti*. As has been pointed out by Pesta, 1915, p. 113, the remainder of the material labelled as "*P. setiferus*" from Rio by Heller is referable to the *P. brasiliensis* group. Following Heller, the range of *P. setiferus* has been universally considered to be from the United States to Brazil, until the recent separation of *P. schmitti*.

Despite doubt as to the precise nature of the Linnean types, usage would seem to make desirable retention of the name *Penaeus setiferus* for one of the Atlantic

American species with short adrostral carinae. Inasmuch as definite records of "*Penaeus setiferus*" from areas outside of the present known range of the northern species did not appear in the literature until relatively very late, it has seemed proper to restrict the Linnean name to the northern species.

A note upon *Penaeus orbignyanus* Latreille may finally be offered. According to the description, this was a specimen of *Penaeus* with short adrostral sulci taken on the coast of the French department of Vendée by "Dr. d'Orbigny." C-M. D. d'Orbigny seems at about this time to have been living in LaRochelle; and as he seems never to have visited regions of the world where prawns consonant with the description of *P. orbignyanus* are known to exist, there is thus no internal evidence against the Biscayan provenance attributed to the specimen by Latreille. However, no confirmation of the record has ever been obtained, and it thus seems necessary to conclude either that an individual from America had drifted across the Atlantic, or that Latreille's specimen, though sent from La Vendée, had been *captured* elsewhere. In the first case, *Penaeus setiferus* s. s. seems the more likely form to reach the Bay of Biscay; in the second it is not possible to judge whether Latreille's description refers to *P. setiferus*, *P. schmitti*, *P. vannamei*, or possibly even to a somewhat atypical individual of one of several Indo-Pacific forms. *P. orbignyanus* thus seems, if not a synonym of *P. setiferus*, to be indeterminable in absence of the type; which according to Dr. Monod and Dr. Dollfuss cannot be found in Paris, and according to Dr. Gordon is not at the British Museum.

DISTRIBUTION: The critical records of *Penaeus setiferus* s. s. available to me may be summarized as follows: Atlantic coast of the United States from Fire Island, New York, to Cape Canaveral, Florida; Gulf of Mexico from Pensacola, Florida, to Timbalier Bay, Louisiana, Texas, and Vera Cruz, Mexico; Cuba; Jamaica. The lack of records between Cape Canaveral and Pensacola, Florida appears to coincide with an actual absence of members of the Division. In the lack of other material than the single specimen in the Berlin Museum, taken by Gundlach, it is impossible to say whether some records of *Penaeus* with short adrostral sulci from Cuba may refer to *P. schmitti*, but it seems possible that they do. The southern species, *Penaeus schmitti*, has been recorded from Rio de Janeiro, Panama, Jamaica, and Haiti by Burkenroad, 1936b. The following fresh material, for the opportunity to examine which I am much indebted to the authorities of the museums concerned, may now be listed; in addition I have now seen much additional material from Rio de Janeiro.

2 ♀, carapace 24–30 mm.; Haiti; Un. Zool. Mus. Copenhagen.
4 ♀, carapace 34–42 mm., 1 impregnated; outside of Kingston Harbor, Jamaica; B. M. (N. H.) 1905. 6. 29. 6–9.
2 ♀, carapace 38–42 mm.; St. Domingo, W. I.; B. M. (N. H.) 1906. 6. 15. 2–3.
1 ♂, adult; St. Thomas; Nat. Hist. Mus. Wien.
1 ♂, carapace 31.5 mm.; Cayenne; B. M. (N. H.) 90. 10. 7. 306.
1 ♀, carapace 18 mm.; Cayenne; Un. Zool. Mus. Copenhagen.
1 ♂, 1 ♀, carapace 29.5 mm.; Maruim (north of Bahia, Brazil); Un. Zool. Mus. Copenhagen.

Many ♂ ♀, juv. to adult; Santos; Zool. Samml. München.
1 ♂, adult; Paranagua; Zool. Samml. München.
2 ♀, juv.; Sta. Catharina; Nat. Hist. Mus. Berlin.

It seems possible that the occurrence of *Penaeus setiferus* is conditioned by salinity within an extreme range governed by temperature; since its distribution seems correlable with that of water of less than 35% salinity within the region where the temperature is at some time in the year less than 25° C. and more than 20° C. (according to Schott, 1926). That this correlation is more than a coincidence is however uncertain; since the distribution of *P. schmitti* is by no means so easily referable to the affects salinity and temperature, this species being known from the very low salinities of Panama as well as from the very high ones of Bahia; and being absent (so far as is known) not only from Vera Cruz where *P. setiferus* occurs but from southern Florida where the North American form has not been taken.

The geographical range of *P. setiferus* corresponds quite closely to that of *P. aztecus* Form A, although the former seems to differ from the latter in its presence in Jamaica and in its lesser extension north of Cape Hatteras (as well as in its lesser bathymetric range and lesser degree of adult independence of the coastal area). So far as present knowledge goes, *P. schmitti* agrees rather well in distribution with *P. aztecus* Forms B and C combined, except that it seems not to range south of Rio Grande do Sul and is not known from Cuba and southern Florida.

Natural History: That *Penaeus setiferus* might have a bathymetric range exceeding that of the commercial fishery off the Mississippi, spawning ground lying in the deeper portion of its range, and a life-span including more than one spawning, has been suggested by Burkenroad, 1934a, p. 81, as a possibility requiring consideration "Even though the adults should actually never reappear in the fishery." That individuals past their first spawning might in fact compose a part of the commercial catch has, although not explicitly, so stated, been the clearly implied belief of Viosca (1920, p. 122) and of Burkenroad. In a preliminary report of their investigations, Weymouth, Lindner and Anderson, 1933, incline to the view that the life-span of *Penaeus setiferus* is only one year, that its entire life is spent in the shallower water, and that the yearly disappearance of adults from the commercial catch corresponds to the natural death of the year-class following spawning. In various recent statements on the shrimp investigations conducted by the U. S. Bureau of Fisheries, however, the opinions of Viosca and of Burkenroad seem to have gained acceptance. Concrete evidence in favor of these opinions would appear finally to be provided by the material here reported upon, the first to become available from areas lying beyond the range of the commercial fishery.

In none of twelve hauls in depths of from 40 to 70 fathoms, made by "Atlantis" during March and April, 1937, was *Penaeus setiferus* taken; and since *P. aztecus*, a species of size and strength equivalent to that of *P. setiferus*, occurred in eleven of these twelve hauls, it seems a safe assumption that, during the season of investigation, *P. setiferus* does not occur at depths greater than 40 fathoms. One catch of 15 specimens of *P. setiferus* was taken, together with 12 of *P. aztecus*, at a depth of 35–39 fathoms; of the other two hauls made in 31–40 fathoms, both yielded *P. aztecus*. Two catches, of 188 and of 57 specimens of *P. setiferus* (the smaller catch being accompanied by 32 specimens of *P. aztecus*) were taken at depths respectively of 25–29 and of 30 fathoms; of the other three hauls made in 21–30 fathoms all yielded *P. aztecus*. Four catches, of 1, 17, 40 (accompanied by 13 of *P. aztecus*) and *ca.* 600[1] individuals of *P. setiferus* were taken at depths of 10–20 fathoms; of the other four hauls at these depths, two yielded *P. aztecus* and one *P. duorarum*. Stations where *P. setiferus* was taken showed no clear distinctions in bottom temperature and salinity from those within the same depth-range where *P. aztecus* but not *P. setiferus* was taken. The extremes of bottom temperature at stations where *P. setiferus* occurred were 16.9°–19.8° C.; of salinity 35.52–36.4°/₀₀.

No striking distinctions were observed between the samples of *P. setiferus* from depths of $\leqq$ 20 fathoms and from $>$ 20 fathoms in size, sex-ratio, or sexual condition; although in the single small catch from more than 30 fathoms (of 2 ♂ and 13 ♀) the minimum size in both sexes (carapace length 34 mm. in males, 38 mm. in females) was greater and the proportion of males was lower than in any of the other samples. The total available range in carapace length was from 27 mm. to 48.5 mm. in females; from 25.5 mm. to 42 mm. in males. Mean carapace length in the most extensive sample (94 ♂, 196 ♀ examined, from 12.5 fathoms, St. 2839) was roughly estimated to be about 36.3 mm. (= *ca.* 160 mm. total length) in females, 35.4 mm. in males; 43 females of this catch attained or exceeded 40 mm. (= *ca.* 170 mm. in total length). The mean in females seemed about the same in the next most extensive sample (66 ♂, 112 ♀, 25–29 fathoms, St. 2820); 20 females of this catch attained or exceeded 40 mm.

Of 259 females from all hauls closely examined, 145 (ranging in carapace length from 29.5 mm. to 48.5 mm.) showed signs of having been impregnated; the range in proportion of impregnated to unimpregnated per sample was from 27 : 1 (Station 2853 No. 12, 30 fathoms) to 1 : 6 (St. 2828, 10.5 fathoms), no clear correlation with depth of capture, with size, or with ripeness of ovary being shown. Soft- and paper-shelled individuals showed no traces of impregnation, so that mating is in this species apparently not an accompaniment of the molt. It must be noted that an entire and undamaged pair of spermatophores was not found attached to a single one of the individuals termed *impregnated*. In a few specimens, a large part of the anterior holdfasts of the spermatophores (comprising the lateral spurs caught between the third and fourth legs and the glutinous median mass between the coxae of the third legs; *cf.* Burkenroad, 1934a, fig. 6) remained; in the rest, more or less extensive traces of the glutinous median mass adhered quite firmly between and anterior to the coxae of the third legs. The clean and shining cuticle of presumably virginal (as regards period since last molt, at least) females was easily distinguishable at a magnification of 12.5×. According to notes on catches of *P. setiferus* made to westward of the Mississippi in depths of less than 10 fathoms in July, 1930 and May, 1931, which included a number of females with undamaged spermatophores, none was observed to bear a trace or part only of a spermatophore. The possibility has therefore been considered that loss of the spermatophores formerly present in the "Atlantis" catches might have been a normal and not an accidental process; and accordingly, careful examination of the sternal recesses and of the oviducts has been made to the end of discovering sperm-storage other than by means of the spermatophores. However, although a few spermatozoa were found among the setae of the third legs in certain of the individuals showing traces of spermatophore attachment, the results of this search were negative (whether among those females showing traces of spermatophore attachment, those without such traces, those with ripe eggs, those with unripe eggs, those hard-shelled or those soft-shelled). It is therefore concluded that the spermatophores in those of the "Atlantis" females which show traces of their former presence have been lost by accident. Since fragments or traces of the holdfasts of the spermatophores remain quite firmly adherent in the material studied; since in many cases setae seem to have been torn out with the spermatophores; and since the impregnated individuals range in degree of maturation of the ovary from very unripe to very ripe, it seems probable that the accidental loss of the spermatophores was a result of the violence of capture, especially in deep water; and that under normal circumstances the spermatophores may be retained for considerable periods. What proportion of individuals in the commercial catch at various seasons may be found on close examination to bear traces of impregnation is not yet known.

---

[1] A random sample of this catch amounting to five gallons or 290 individuals was preserved and has been available for laboratory investigation. All other catches were preserved entire.

Of 240 females in which the ovary was closely examined, the eggs were very ripe in 40, ripe to moderately unripe in 150, very unripe in 50.[1] No ovaries were seen which seemed to have been very recently emptied. The smallest females with eggs extremely ripe have a carapace length of 30 mm. No striking differences in range of maturation of the ovary were observed between the impregnated and the unimpregnated or the larger and the smaller individuals, nor between the samples from deeper and those from shallower water. In two individuals (from St. 2820, 25–29 fathoms) with very unripe ovary, respectively of carapace length 37 mm. and 38 mm., a few of what appear very definitely to be degenerated ripe eggs in process of resorption (a thin spherical membrane enclosing a cortex of clear cylinders and a central granular mass) were noted to be scattered among the developing young ova. Since the method of examination employed (inspection of the ovary through a cut in the second pleonic somite, at magnifications of 12.5 × to 30 ×) would reveal the old eggs only in very unripe ovaries where the contrast is great; since resorption might be expected to continue beyond the point of detection with ripening of the ovary; and since, according to the condition in spent females of *P. aztecus* (*vide* p. 49) the proportion of unshed eggs remaining after spawning is variable, frequently nil, it is probable that the number of individuals detected is by no means commensurate with the number which have spawned on a previous occasion.

---

[1] Eggs termed "very ripe" are those about .20 mm. to .30 mm. in greatest dimension (mean spherical diameter probably about .25 mm. or less), light yellow to light orange in color (in formalin), and with the cortex of the egg composed of radially arranged columns of clear stiff material embedded in a granular matrix (an appearance also easily recognized in fresh material, according to notes made in 1931). In eggs termed "ripe," the size may be little less than in the above and the color yellow, but the substance of the egg is simply granular, without columnar structure. In less ripe eggs the size is smaller and the density of granulation less; down to the smallest considered, about .08 mm. in greatest dimension, packed together with many still smaller cells in a slender, colorless ovary.

The fact that no recently spent females were taken by "Atlantis" seems to indicate that spawning had not yet begun by April 10th (accepting that the resorbing eggs detected in the unripe ovaries provide indication that spawning may, on occasion at least, be survived and repeated); the relatively low proportion (1/6) of individuals with extremely ripe ovaries as compared with those moderately ripe (3/5) is not in conflict with this assumption. Accepting that spawning had not yet begun, it would appear that the eggs are not necessarily shed immediately upon their attainment of columnar structure; and it is even possible that still riper stages, distinguishable by a difference in color or in some other way, may occur before the time of spawning (although it may be remarked that no further stage of maturity was discovered in *P. aztecus*, where spawning seems to have been in progress in the population examined). Since as mentioned above the ovaries of impregnated females range from very unripe to very ripe, it would appear that mating has no close relation to imminence of spawning (as also in the *Penaeus brasiliensis* group; *vide* p. 50) and the material taken by "Atlantis" thus does not serve strictly to define the areas of spawning. Since spent females have not been detected in the commercial catch (that is, in depths of 15 fathoms or less) at any season (Burkenroad, 1934a), it seems possible that the ripe females taken by "Atlantis" in 10–15 fathoms would have moved farther off-shore to spawn;[1] in this case the proportion of ripe to unripe females might be expected to increase with depth in a fashion not clearly indicated by the available catches but perhaps demonstrable later in the year.

According to the present observations, very few individuals of *P. setiferus* of size less than that at which maturity may be attained occur at depths greater than 10 fathoms in the region of the Mississippi River during early spring. The population found beyond 10 fathoms appears to be most dense at depths of less than 20 fathoms but to range out to 40 fathoms; that is, to a limit about two and one-half times as great as the deepest previous records (15 fathoms, the maximum depth in which the commercial fishery has regularly operated in Louisiana). If the commercial "spring run" of "lobster-shrimp" (which seems to have appeared in the fishery in 1937 before the time at which the operations of "Atlantis" were begun) should be considered to correspond to an on-shore movement of individuals which have wintered in deeper water, it seems possible that during the winter the density of population in depths of more than 20 fathoms may be greater than at the time of investigation by "Atlantis." Since the bathymetric limit of the species can be definitely stated to lie considerably outside the limits of the commercial fishery, it seems by no means impossible that the larger individuals, which after appearing in the fishery in quantity in spring, disappear again by winter, may in the course of the summer simply have returned to spawning and wintering grounds at depths beyond 15 fathoms.

---

[1] As regards the claim of Pearson, 1935, to have discovered eggs of *P. setiferus* floating at the surface in water only 5 fathoms deep off Georgia, see p. 52 below.

It seems possible that the "Atlantis" catches of *P. setiferus* in Louisiana may correspond in a general way to a seaward extension of the upper mode at about 150 mm. shown by Weymouth, Lindner and Anderson (1933, fig. 10) in the commercial catch in Georgia in late March and early April, 1931. Thus, if the length-frequency curves for the Georgia catches are accepted (as by their authors) to refer simply to the growth of a single year-class, it would seem necessary to consider the "Atlantis" catches as composed entirely of individuals born during the preceding summer and approaching their first spawning. On the other hand, it would seem within possibility that the distinct bimodality indicated in the material from Georgia during winter and early spring (referred to by the authors of the curves as a lack of distinct mode) might be interpreted in terms of a lower mode composed of individuals which have not, an upper one chiefly of individuals which have previously spawned. The size of the smallest sexually active females in the "Atlantis" catches, 30 mm. carapace length (*ca.* 130 mm. total length, corresponding to a weight about one-third that of the largest females of 190 mm.), does not conflict with this interpretation; and the indication (according to the presence of resorbing eggs in unripe ovaries) that some individuals of total length less than 165 mm. in the "Atlantis" catches have spawned on a previous occasion is distinctly in accord with it. If this view of the significance of the upper mode in early spring in Georgia should be accepted, it might be thought that the various movements of the modes in the account cited, some of them sudden and peculiar, might refer in part not to growth but to movements comparable with the on-shore spring run and the off-shore spawning movements tentatively accepted above for the Louisiana population.

Since the present observations seem to demonstrate a need for means of determining the bathymetric derivation of components of the population of

Penaeus setiferus, such as cannot be met by tagging (because of the limitation to the shallow part of the range of the species of a fishery adequate to supply a return of the tags), a method by which it may prove possible to identify the position of an individual at its last molt is here suggested. In the majority of decapod crustacea a balancing organ is present in the base of the antennule, consisting of a closed or open pocket which in many cases contains a concretion or statolith. In the Penaeidea a statolith is invariably present, which is among the forms of exclusively natant life a self-secreted pellet of cuticular material, but which among the forms normally coming into contact with the substratum is composed of a mass of small objects introduced from the exterior at the molt and more less conglomerated by cuticular secretion. The nature of the statolith has already been employed (by Burkenroad, 1936, pp. 22, 106 and 1937, p. 512) for demonstration of an essential dependence upon the substratum in supposedly holonektonic peneids. In a similar manner, it seems possible that to the degree to which particular areas of bottom may possess peculiarities of a nature to be reflected in the statolith of individuals of a species molting there, these individuals might remain distinguishable until after the next molt even after extensive movement and mixture with individuals from other areas.

The statolith of *Penaeus setiferus* is chiefly composed of siliceous granules, together with some fecal pellets of small organisms, and more rarely calcareous fragments and foraminiferal and radiolarian tests; it therefore shows no plain indication of selective gathering as to material included. Since the sandgrains included may be either large or small, the statolith shows no plain indication of selective gathering as to size, within wide limits. In samples of *P. setiferus* from shallow water (as from Pensacola Bay, 6 fm.; and St. 2839, 12.5 fm.) the bulk of the sand grains of the statolith are, with considerable constancy from individual to individual, of large size, approximately .05 mm. in mean diameter. On the other hand, in samples from deep water (as St. 2820, 25–29 fm.; and St. 2822, 35–39 fm.) all of the granules are of very small size, about .01 mm. in mean diameter (as might be expected from the probable concentration of large granules in shallow water deposits), giving the statolith in these samples a very characteristic appearance. Finally, in one sample (St. 2829, 10.5 fm.), statoliths composed either of large or of small grains (but not of both) were noted; a state of affairs presumably referable to the presence of individuals recently arrived from deep water. In the statolith of *P. aztecus* from depths of more than 50 fathoms, the occurrence of foraminifera was observed to be much more freqent than in material of this species from shallower water; and possibly characteristic local differences in proportion of fecal pellets included were in the statolith also noted.

In areas where horizontal movement of *P. setiferus* (or other decapods) might carry individuals from one drainage system to another, and where the deposits of the different systems might be mineralogically distinct, it seems possible that the method of statolith examination might also prove useful for determination of horizontal movement. Further study of the method is in progress.

Division II

Distinctions between Division 1 and Division 2 of *Penaeus;* and between the section of Division 2 comprising the Indo-Pacific and Mediterranean forms and the characteristically American section, have been discussed by Burkenroad, 1934a, p. 74. Further studies of *Penaeus* indicate a need for modification of details of this statement, but the general outline remains serviceable.

Since its establishment by Latreille in 1817, until the present, the name *Penaeus brasiliensis* has been universally applied to all Atlantic material (and by certain students to all Pacific American material also) of that section of the Division in which the supraorbital carina of the carapace is not recurved upon itself posteriorly. A variety from Vera Cruz, *P. brasiliensis aztecus*, was distinguished by Ives, 1891, p. 190, by means of a worthless criterion (length of antennal flagella); this name was considered a synonym of *P. brasiliensis* by Burkenroad, 1934a, p. 94, who was unable to discover any sharp differences between specimens from North Carolina, Louisiana, Colombia, Cuba, and Africa, although finding Atlantic to be distinct from Pacific American material. However, the examination since 1934 of a large assortment (including more than 1000 individuals) of the *Penaeus brasiliensis* group now permits the distinction of three Atlantic and two Pacific American species (the latter of which have been defined, under the names *P. brevirostris* Kingsley and *P. californiensis* Holmes, by Burkenroad, 1938). In the light of present knowledge, it appears that the three African juveniles and the Cuban specimen discussed in 1934 belong to other species than the bulk of the then available Atlantic material; and also, although this step might be avoided by judicious selection of a holotype, it is found proper to retrieve and define the name introduced by Ives.

In this matter of names for the newly distinguished Atlantic species of the *P. brasiliensis* group, two conspecific ancient specimens (one dry, one in spirit) labelled "*Penaeus brasiliensis*. Brazil. Given by the Museum of France. Mus. Leach" have been examined during a recent visit to the British Museum. There is an entry corresponding to these specimens (or to one of them) in the MS Register of the collection [which according to information kindly supplied by Dr. Gordon probably dates from *ca.* 1826], as well as in the Catalogue published in 1847. According to Dr. Gordon, Leach's collection was acquired by the British Museum in 1826, that is, within nine years of the description of *P. brasiliensis*. An enquiry by Dr. Th. Monod of the Paris Museum has failed to discover Latreille's types in that institution, a result corresponding to the probability that the remarks on *P. brasiliensis* by H. Milne-Edwards, 1837, are not based on the examination of material. It therefore seems quite possible that the two specimens in the British Museum comprise Latreille's types; but in order to set this point completely at rest, the spirit specimen, a small but adult female in fairly good condition, is (even though the action may be a redundant one) designated below as neotype of *Penaeus brasiliensis*. An examination of the types of

Penaeus brasiliensis aztecus Ives, made available by the Philadelphia Academy of Natural Sciences, indicates these to consist partly of *Penaeus setiferus* (Linn.), but in the main of a species of Division 2 distinct from the neotype of *P. brasiliensis*, from which a holotype is designated below. *Penaeus aztecus* therefore becomes the name of the species of "*P. brasiliensis*" most abundant in North America. Finally, no name is available for the third Atlantic form, which is accordingly described below as *P. duorarum* n. sp.

It is not only possible to separate "*P. brasiliensis*" into several species, but also to distinguish in *P. duorarum* two, in *P. aztecus* three forms or subspecies which are described below under alphabetical designations. These forms are quite well-defined, and while they have zoological ranges for the most part distinct, "Form B" of *P. aztecus* overlaps "Form A" in Cuba and "Form C" at Rio de Janeiro. It therefore seems possible that the various forms should be considered as distinct systematic units and should be named as subspecies accordingly; but until further information as to the natural history of the group is available, this step may be postponed.

The relatively very extensive representation of Atlantic forms of the *P. brasiliensis* group herein brought together reveals quite clearly that remarkable differences exist between the three species in distribution. For opportunity to examine that considerable portion of the material not collected during expeditions of the Bingham Oceanographic Foundation, thanks are due to several donors listed after the citations *B. O. C.;* as well as to the institutions cited by the abbreviations *A. M. N. H.* (American Museum of Natural History); *B. M. (N. H.)* [British Museum (Natural History)]; *D. T. R.* (Department of Tropical Research, New York Zoological Society); *I. M. Z. U. T.* (Istituto e Museo di Zoologia della R. Universitá, Torino); *M. C. Z.* (Museum of Comparative Zoology, Harvard); *M. C. S. N. M.* (Museo Civico di Storia Naturale di Milano); *N. M. W.* (Naturhistorisches Museum, Wien); *P. A. N. S.* (Philadelphia Academy of Natural Sciences); *P. M. N. H.* (Department of Zoology, Peabody Museum of Natural History); *U. Z. M. C.* (Universitetets Zoologiske Museum, Copenhagen); *Z. M. U. B.* (Zoologisches Museum der Universität, Berlin); *Z. S. S. M.* (Zoologische Sammlung des Staates, München).

Penaeus brasiliensis Latreille, restricted

Figures 16, 17, 22

? *Penaeus brasiliensis*, Latreille, 1817, p. 156.
P. brasiliensis, auct., part; Andrews, 1911, fig. 3.

MATERIAL:

ATLANTIC SOUTH AMERICA

2 ♀. *B. M. (N. H.)*. TYPES? (NEOTYPE). "Brazil. Given by the French Museum. Mus. Leach."

28 ♂, 21 ♀. *B. O. C. 318*. Rio de Janeiro, Brazil. Market (?); May (?). Mr. M. W. Feingold, from Dr. C. Moreira.

1 ♀. *P. M. N. H. 161.* Rio de Janeiro, Brazil.
3 ♂, 2 ♀. *Z. M. U. B.* Rio de Janeiro. Selenka.
1 ♀. *Z. S. S. M.* Rio de Janeiro. Selenka.
1 ♀. *Z. S S. M.* Rio de Janeiro, Essendorfer.
1 ♂, 7 ♀. *N. M. W.* Rio de Janeiro. "Novara."
2 ♀. *N. M. W.* Bahia. "Saida."
1 ♂, 1 ♀. *M. C. Z.* Bahia, Brazil. Hartt.

CARIBBEAN and ANTILLES

1 ♂, 2 ♀. *P. M. N. H.* Sabanilla, Colombia. Shore, March 16–24, 1884. "Albatross."
1 ♀. *U. Z. M. C.* St. Thomas. Riise.
2 ♂, 1 ♀. *U. Z. M. C.* St. Croix. Kröyer.
3 ♂. *D. T. R.* Bizeton, Haiti. March 1, 1927.
1 ♂. *B. O. C. 9.* Havana Harbour, Cuba. February 1, 1932.
3 ♂, 4 ♀. *Z. M. U. B.* Cuba. Gundlach.
1 ♀. *N. M. W.* West Indies.

ATLANTIC NORTH AMERICA

1 ♂. *P. M. N. H.* Atlantic off Cape Hatteras (35° 21′ N., 75° 24′ W.). 13 fathoms, October 19, 1874. "Albatross" St. 2285.

BERMUDA

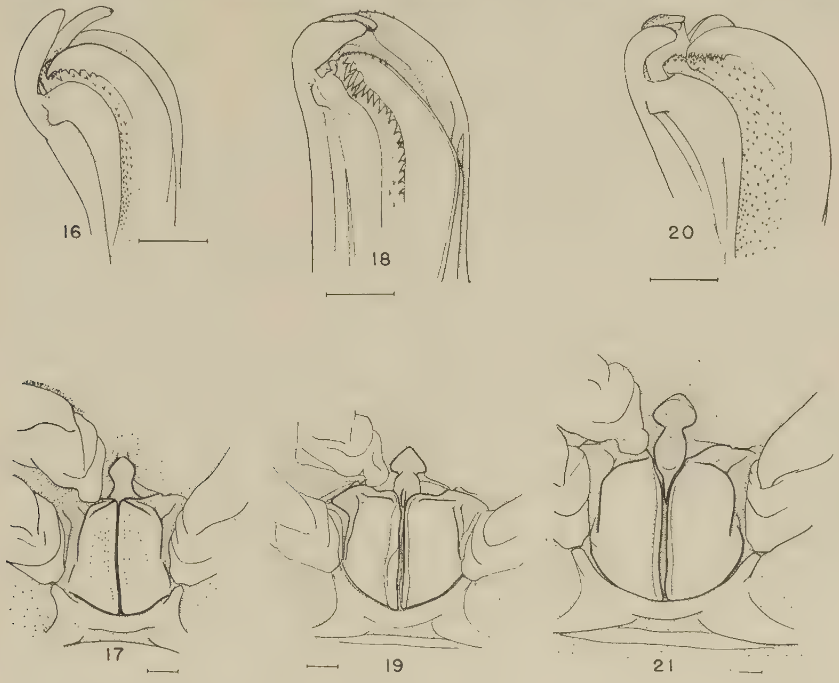
1 ♀. *B. O. C. 319.* Mullet Bay. January 27–29, 1935.
1 ♀. *B. O. C. 320.* Ferry Reach. Surface, at light. April 24, 1936.
1 ♂, 3 ♀. *M. C. Z. 9283.* Ferry Reach. Surface, at light. August, 1935. Wheeler.
1 ♂, 1 ♀. *P. M. N. H. 592.* Port Royal Bay. Seine. September 21, 1905.
1 ♀. *P. M. N. H. 3116.* Bermuda. April, 1898. Jones.
1 ♀. *D. T. R. 301363.* Bermuda. 1930.
1 ♀. (with cast shell). *D. T. R. 3130 and 3131.* Bermuda. 1930.
1 ♀. *P. M. N. H. 3116.* Bermuda. April, 1892.

The largest female has a carapace length of 38 mm., a total of about 163 mm., the largest male a carapace of 29 mm.; these are from *B. O. C. 318*, Rio de Janeiro. The smallest females of the same sample have a carapace of 12 mm., the smallest males of 11 mm. The smallest impregnated female of this sample has a carapace of 28 mm.; the smallest male with joined petasmal endopods, of 23 mm.

The largest of the available northern females, of carapace 28 mm., is impregnated, as is also another of 24 mm. The smallest northern male with joined petasmal endopods has a carapace of 17 mm.

Diagnosis: Posteromedian part of the median plate of sternite XIII of the females without other longitudinal carination than a very small knob-like projection from the posterior edge. Lateral plates of XIV of adult females meeting in the midline anteromedially, their anteromedian corners being produced forward so as to conceal completely the posteromedian part of the median plate of XIII.

Medially curved distal end of the heavily chitinized distoventral lobes of the adult petasma terminates as a rather projecting tip free of the membraneous distolateral lobe; external edge of the distoventral lobes unarmed; median (or, in consideration of the curvature of the lobes, proximal) anterior edge of the distoventral lobes, near the distal end, with a well-spaced series of three to nine sharp and slender teeth of moderate size, similar to but larger than the neighboring armature of the anterior surface of the distolateral lobes. The fold of the free margin of the distolateral lobe, just median to the tip of the distoventral lobe, projects posteriorly as a large fleshy flap bearing an extensive and conspicuous spinous armature. The distomedian lobes of the petasma are quite long.



Figures 16–21

Penaeus brasiliensis Latreille (restr.). **16.** Petasma (distal part, anterior view from right side), ♂ of car. 28 mm. (Brazil, *B. O. C.* No. 318), × 9. **17.** Thelycum; ♀ of car. 26 mm. (Brazil, *B. O. C.* No. 318), × 4.

P. duorarum, n. sp. **18.** Petasma; ♂ of car. 25 mm. (Haiti, D. T. R., N. Y. Z. S.), × 9. **19.** Thelycum; ♀ of car. 24 mm. (Havana, *B. O. C.* No. 298), × 4.

P. aztecus Ives (restr.). **20.** Petasma; ♂ of car. 31 mm. (Louisiana, *B. O. C.* No. 31), × 9. **21.** Thelycum; ♀ of car. 31.5 mm. (Louisiana, *B. O. C.* No. 260), × 4. Length of 1 mm. indicated at each drawing.

Adrostral sulci of the carapace well defined posteriorly; usually about equal in breadth to the median carina which separates them (measured at a point a little before their posterior ends). Median carina sharply and continuously sulcate. Supraorbital carina well defined, its weak anterior part shorter than the sharper posterior part. The carina forming the posterodorsal border of the antennal sulcus usually extends to within about one-third its own length of the orbital angle. Rostrum usually to the end of the antennular peduncle, armed above with 8 to 12 teeth, usually 9 or 10. Dorsolateral sulci of the sixth pleonic somite from one-fifth (or less) to three-fifths as wide as the interval separating their dorsal lip from the midline (measured at a point about one-third in advance of the posterior end); usually widely open in Brazilian material, often very narrow or even completely closed in northern material, but ranging to as narrow as two-fifths in the former, and to as broad as three-fifths in the latter.

Third legs rather short, reaching from to the middle of the second segment of the antennular peduncle to the length of the dactyl beyond the peduncle (slightly longer in juveniles than in adults); often not to the end of the peduncle in Brazilian material, often beyond it in more northern specimens.

REMARKS: *Penaeus brasiliensis* as here restricted most nearly resembles the Pacific American species *Penaeus californiensis* Holmes (Burkenroad, 1938, p. 67). Like that form it is distinguished from all of the other American species of the group by the extended anteromedial corners of the lateral plates of its adult thelycum; and by the projecting tip of the distoventral lobe of its petasma, and the large size and conspicuous armature of the posteriorly protruding fold of the distolateral lobe. *P. brasiliensis* is distinguished from *P. californiensis* by the less extensive carination of the posteromedian part of the median plate of its thelycum (which in the latter form bears a well-defined ridge running anteriorly from the posteromedian knob which is alone represented in *P. brasiliensis*); and also by the usually blunter and shorter free tip of the distoventral lobe of its petasma, and the modally more numerous spines which arm the anteromedian edge of this lobe.

Although the adult genitalia are recognizable at a glance, it is rather difficult to distinguish sexually undeveloped specimens of *P. brasiliensis* from those of related Atlantic species, since the more or less constant non-genital distinctions, which make easier the recognition of juveniles of the two Pacific American species, seem not to be developed among the Atlantic forms. The most useful criteria are the following: down to a carapace length of 12 mm. at least, some trace of a median carina is visible on the posterior part of the median plate of females of *P. aztecus* and *P. duorarum;* thus all but the smallest juvenile females of these two forms may be separated from *P. brasiliensis* (which never has the ridge). Some trace of the spinules which arm the external margin of the distoventral lobe of the petasma of *P. duorarum* is visible down to a carapace length of 12 mm. at least, so that all but the smallest juvenile males of this species may be separated from *P. brasiliensis*. Juvenile males of *P. brasiliensis* may frequently be differentiated from *P. aztecus* in the North American region by the usually narrower sulci of their sixth pleonic somite; in the Caribbean area by their broader adrostral sulci and well-defined, continuous median carapacic sulcus; in Brazil by their usually broader sixth pleonic sulci and well-defined, continuous median carapacic sulcus.

Penaeus duorarum, n. sp.

Figures 18, 19, 23, 25, 26, 27

MATERIAL:

Form A

GULF OF MEXICO

2 ♂, 2 ♀. *B. O. C. 301.* (HOLOTYPE and COTYPES). Off Alabama ("Atlantis" St. 2813). 19 fathoms, March 20, 1937.
1 ♀. *B. O. C. 6.* Pensacola Bay, Florida. February 20, 1932.
2 ♂, 1 ♀. *B. O. C. 7.* Pensacola Bay. March, 1932.
2 ♂, 1 ♀. *B. O. C. 302.* Pensacola Bay. 5 fathoms, March 11–16, 1935.
2 ♂, 2 ♀. *B. O. C. 303.* Off Pensacola Bay. 5 fathoms, March 23, 1935.
3 ♂, 6 ♀. *B. O. C. 304.* Off Englewood, Florida. 4 fathoms, January 7, 1936. Bass Biological Station.
2 ♂, 5 ♀. *B. O. C. 305.* Off Englewood. 4 fathoms, January 14, 1936. Bass Biological Station.
20 ♂, 5 ♀. *B. O. C. 306.* Sanibel Island, Florida. Shore, June, 1935. Miss M. Storey.
1 ♀. *P. M. N. H.* Tortugas Islands, Florida.
1 ♀. *M. C. Z. 1521.* Tortugas Islands. Whitehurst.
1 ♀. *M. C. Z. 1301.* Tortugas Islands. Holder.
2 ♂, 1 ♀. *M. C. Z. 4384.* West of Tortugas Islands (24° 36′ N., 84° 05′ W.). "Blake" St. 29. "955 fathoms" [!].
1 ♂. *U. Z. M. C.* Vera Cruz. Liebman.
2 ♂, 1 ♀. *M. C. Z. 4170 and 7211.* Alacran Reef (4 miles west of Whale Rock), Campeche Bank, Mexico. "Blake" St. 37, 35 fathoms.
1 ♀. *B. O. C. 5.* Double-Headed Shot Cay, Straits of Florida. 3 fathoms, March 7, 1925. "Pawnee II."

ATLANTIC NORTH AMERICA

1 ♂. *B. O. C. 307.* Key Largo, Florida. March 19, 1934. Mr. M. B. Bishop.
3 ♂, 2 ♀. *B. O. C. 13.* Off Miami Beach, Florida. Surface, February 21, 1927. "Pawnee II."
3 ♂, 2 ♀. *P. M. N. H.* Mouth of Indian River, Florida. March 21, 1874. Palmer.
1 ♀. *P. M. N. H.* Indian River.
1 ♂. *B. O. C. 88.* Off Matanzas Inlet, Florida. 8–10 fathoms, April 2, 1934. Mr. M. B. Bishop.
1 ♂. *M. C. Z. 1522.* Charleston, South Carolina.
8 ♂, 2 ♀. *P. M. N. H.* Fort Macon, North Carolina. Yarrell.
1 ♀. *P. M. N. H.* Fort Macon. Contes.
1 ♀. *P. M. N. H.* Off Cape Hatteras, North Carolina. (35° 21′ N., 75° 25′ W.). 11 fathoms, October 19, 1874. "Albatross" St. 2286.

BERMUDA

1 ♂. *B. O. C. 308.* Mullet Bay. 3 feet, January 27, 1935.
2 ♀. *B. O. C. 309.* Ferry Reach. Surface at light, 1936.
1 ♂. *P. M. N. H. 857.* Gilbert Island Bay. November 19, 1905.
1 ♀. *P. M. N. H.* Fairyland Creek. Seine, November 30, 1915.

Form B

CARIBBEAN and ANTILLES

1 ♀. *B. O. C 298.* Havana Harbor, Cuba. February 1, 1932. "Mabel Taylor."
1 ♂. *B. O. C. 221.* Guantanamo Bay, Cuba. April 22, 1933. "Atlantis."

1 ♂, 1 ♀. *N. M. W.* Cuba. Poppig.
1 ♂, 12 ♀. *Z. M. U. B.* Cuba. Gundlach.
1 ♂. *B. O. C. 10.* Siguanea Bay, Isle of Pines. April 6, 1925. "Pawnee II."
1 ♂, 1 ♀. *N. M. W.* East Mexico. Bilimek.
2 ♂, 1 ♀. *B. O. C. 299.* Turneffe Cay, Gulf of Honduras. April 21, 1925. "Pawnee II."
1 ♂, 6 ♀. *B. O. C. 300.* Kingston, Jamaica. Market, February 1, 1934. "Atlantis."
1 ♀. *P. M. N. H.* Jamaica. March 1–11, 1884. "Albatross."
4 ♀. *D. T. R. 27193.* Port au Prince, Haiti. From gut of fish.
1 ♂. *D. T. R. 27270.* Port au Prince.
1 ♂. *D. T. R. 27402.* Port au Prince. From gut of snook.
1 ♂, 1 ♀. *D. T. R. 27415.* Port au Prince.
12 ♂, 17 ♀. *D. T. R.* Bizeton, Haiti. March 1, 1937.
1 ♂, 1 ♀. *D. T. R.* St. John, West Indies. "Antares."
10 ♂, 12 ♀. *B. O. C. 95.* Limon Bay (mouth of Sweetwater River), Canal Zone. Shore (seine). February 12, 1934.
8 ♂, 4 ♀. *P. M. N. H.* Sabanilla, Colombia. Shore. 1884. "Albatross."

WEST AFRICA

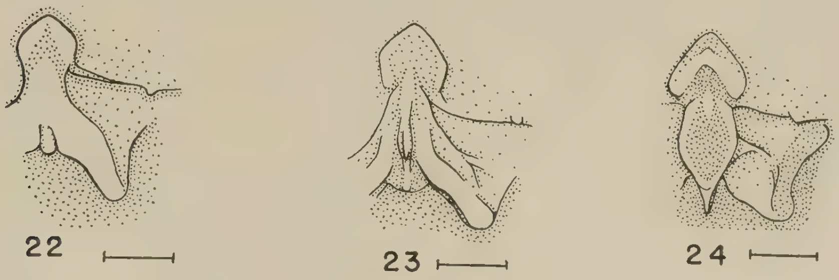
2 ♀. *B. M.* (*N. H.*). Rufisque Island, Senegambia. Maltzan.
4 ♂, 5 ♀. (+ 9 indet.). *B. M.* (*N. H.*). Murray Town, Sierra Leone.
1 ♂. *N. M. W.* Dakar, Senegambia. "Helgoland."
1 ♀. *Z. M. U. B.* Goree, Senegambia. v. Maltzan.
3 ♀. *Z. S. S. M* Keta, Togo.
3 ♂, 2 ♀. *M. C. S. N. M.* Kotonow, Dahomey.
1 ♀. *Z. S. S. M.* Duala, Kamerun. v. Eitzen.
2 ♀. *Z. M. U. B.* Victoria (?), Kamerun.
1 ♀. *M. C. Z. 7240.* Dahomey, West Africa [Lac Ahêmé (?)]. Hubert.
1 ♂, 1 ♀. *B. M.* (*N. H.*). Whydah, Dahomey.
2 ♀. *B. M.* (*N. H.*). Off Lagos. Cadman.
1 ♂, 1 ♀. *A. M. N. H. 4734.* Banana, Belgian Congo. July, 1915. Lang-Chapin Congo Expedition.
1 ♀. *Z. M. U. B.* Congo Mundung. 2/X/1898. D. T. E.
1 ♂. *A. M. N. H. 6930.* Lobito Bay, Angola. May 2, 1925.

In the largest available female specimens, the types from off Alabama in 19 fathoms, carapace length is respectively of 50.8 mm. (total length about 190 mm.) and 48 mm. Males from the same haul measure 37 mm. and 34 mm. Males also of "Form A" from Alacran reef in 35 fathoms measure 39 and 35 mm., the female 42 mm. The female of "Form A" from off Hatteras in 11 fathoms has a carapace of 41 mm. The largest American specimens of "Form B," from Bizeton, Haiti, have a carapace length in females of 34 mm., in males of 25 mm. The largest African female, from off Lagos, has a carapace of 47 mm.; the largest male, from Murray Town, of 26.5 mm.

The smallest males with joined petasmal endopods have a carapace of 15 mm.: the smallest impregnated females, of 23 mm.

Diagnosis: Posteromedian part of the median plate of the adult thelycum with a well-developed undivided longitudinal carina extending anteriorly for a variable distance toward the semicircular anterior part of the elevation. Lateral plates of the adult thelycum a little produced anteromedially but never meeting medially at their extreme anterior ends, being instead somewhat to considerably divergent, and thus clearly exposing the carina of the posteromedian part of the median plate.

Medially curved distal ends of the distoventral lobes of the petasma not projecting free of the distolateral lobes; external edge of the distoventral lobes scabrous, with a series of 2 to 12, usually 4 to 7, spinules which may be minute but are usually distinct even in exceedingly small unjoined petasmata. Median or attached edge of the distoventral lobes, on the anterior side, with a compact group of 6 to 16 very large, long, sharp, curved spines. Fold of the distolateral lobe rather small, protruding very little on the posterior side of the petasma and armed very inconspicuously if at all.



Figures 22–24

P. brasiliensis Latreille (restr.). **22.** Thelycum (posterior parts of median plate of XIII exposed by removal of lateral plates of XIV); ♀ of car. 28 mm. (Brazil, *B. O. C.* No. 318), × 9.

P. duorarum n. sp. **23.** Thelycum (median plate); ♀ of car. 25 mm. (Pensacola, *B. O. C.* No. 7), × 9.

P. aztecus Ives (restr.). **24.** Thelycum (median plate); ♀ of car. 19 mm. (Delaware, *B. O. C.*), × 9. Length of 1 mm. indicated at each drawing.

Third legs moderately short, often rather stout, varying in extent from to the end of the second segment of the antennular peduncle to a chela beyond the peduncle.

In typical *P. duorarum* of "Form A," from North America, Double-Headed Shot Key, and Bermuda, the dorsolateral sulci of the sixth pleonic somite are narrower, and although they may be open to a breadth of one-third the interval to the midline, are characteristically almost or entirely closed. In *P. duorarum* of "Form B," from the Antilles, the Caribbean coasts of North, Central and South America, and from Africa, the dorsolateral sulci of the sixth pleonic somite are broadly open, their breadth being from one-half to more than equal the interval from their dorsal lip to the median line (measured at a point about one-third in front of the posterior margin of the somite.

According to notes made on the freshly-captured specimens, the large adults of *P. duorarum* taken off Alabama were dun-colored, rather than bright orange like *P. aztecus* from deep water.

Remarks: *P. duorarum* is not represented in Pacific America by any species with greater resemblance to it than to the other Atlantic species. It appears to be most closely related to *P. brevirostris* and *P. aztecus*, especially in that the lateral plates of the thelycum do not meet anteromedially to conceal the postero-median part of the median plate, and in that the distoventral lobes of the petasma do not extend free of the distolateral lobes; the carination of the median plate of the thelycum, however, resembles that of *P. californiensis*. In petasma *P. duorarum* perhaps more nearly resembles *P. brevirostris* than *P. aztecus*, in the small size and weak or absent armature of the posterior protrusion of the fold of its distolateral lobe, and in so far as the armature of the external margin of its distoventral lobe may represent extension of the series of one or two spinules found at the distal end of the lobe in *P. brevirostris*.

Juvenile males of *P. duorarum* are recognizable by the development even at very small sizes of the spinose armature of the external margin of the disto-ventral lobe of the petasma. Juvenile females are easily distinguishable from *P. brasiliensis* by the carination of the median plate of the thelycum; from the Pacific relative of *P. brasiliensis*, *P. californiensis*, however, they are not distinguishable at small sizes where (as in all species of *Penaecus* with enclosed thelycum) the lateral plates recede from one another; nor do they differ conspicuously in thelycum from small specimens of *P. aztecus* (and the Pacific *P. brevirostris*) in which the anterior bifurcation of the carina of the median plate is not clearly indicated. Juvenile females of *P. duorarum* from North America ("Form A") may be separated from those of *P. aztecus* of "Form A" from the same region by the fact that the sulci of the sixth pleonic somite of the former are very narrow, those of the latter broad. In the Caribbean, peculiarly enough, this difference is reversed, the pleonic sulci being narrower in *P. aztecus* of "Form B" than in *P. duorarum* of "Form B"; but in this area a clear difference is provided by the narrowed adrostral sulci and shallow discontinuous median carapacic sulcus of "Form B" of *P. aztecus*. *P. duorarum* is absent from South America.

Penaeus aztecus Ives, restricted

Figures 20, 21, 24, 28, 29, 30, 31, 32, 33

Penaeus brasiliensis aztecus, Ives, 1891, p. 190, part.
Penaeus brasiliensis, auct., part; Ortmann, 1891. T. XXXVI, fig. 1c; Burkenroad, 1934a, figs. 8, 9.

Material:

Form A

GULF OF MEXICO

11 ♂, 7 ♀. *P. A. N. S. 61.* (Holotypes and Cotypes). Vera Cruz, Mexico. Heilprin Expedition.
1 ♂. *B. O. C. 30.* Off Pass a Loutre, Louisiana. 12 fathoms, January 1931.
2 ♂, 1 ♀. *B. O. C. 31.* 30 miles south of Barataria Pass, Louisiana. 16 fathoms, August 6, 1930.

97 ♂, 190 ♀. *B. O. C. 257-269.* Off Louisiana. ["Atlantis" Stations 2819, 2823, 2822, 2828, 2830, 2837, 2838, 2840, 2853 (2, 3, 5-13)]. 12-70 fathoms, March 22-April 10, 1937. "Atlantis."

3 ♂, 8 ♀. *B. O. C. 116.* Pensacola Bay, Florida. Shrimp-trawl, September 9-15, 1932.

43 ♂, 55 ♀. *B. O C. 310-312.* Pensacola Bay. 5 fathoms, March 11-16, 1935.

ATLANTIC NORTH AMERICA

2 ♂, 2 ♀. *B. O. C. 313.* Off south shore of St. Augustine, Florida. Shrimp trawl, October 1, 1935. Mr. Y. H. Olsen.

1 ♀. *B. O. C. 314.* Off Charleston Harbor, South Carolina. Shrimp trawl, October, 1935. Mr. G. R. Lunz, Jr. and Mr. Y. H. Olsen.

2 ♂, *P. M. N. H.* Fort Macon, North Carolina Yarrell.

1 ♂. *M. C. Z. 1513.* Great Egg Harbor, New Jersey. Baird.

47 ♂, 38 ♀. *B. O. C.* Delaware Bay and Atlantic coast of New Jersey (Wildwood to Brigantine). 4 fathoms or less, August 26-October 17, 1932. Dr. A. E. Parr.

CUBA

1 ♀. *Z. M. U. B.* Cuba. Gundlach.

Form B

ATLANTIC NORTH AMERICA

1 ♂. *B. M. (N. H.).* "North America. Dr. Yarrell."

1 ♂. *B. O. C. 315.* Key Largo, Florida. March 19, 1934. Mr. M. B. Bishop.

CARIBBEAN and ANTILLES

1 ♂, 1 ♀. *Z. M. U. B.* Cuba. Gundlach.

2 ♂. *N. M. W.* Cuba. "Saida."

1 ♂. *N. M. W.* Cuba. Poppig.

1 ♀. *N. M. W.* East Mexico. Bilimek.

3 ♂, 1 ♀. *B. O. C. 114.* Kingston Harbour (western end), Jamaica. 4 feet, February 1, 1934.

5 ♂, 4 ♀. *B. O. C. 115.* Kingston, Jamaica. Market, February 1, 1934.

1 ♂. *P. M. N. H.* Jamaica. March 1-11, 1884. "Albatross."

1 ♂, 1 ♀. *B. M. (N. H.).* "St. Domingo."

5 ♂, 2 ♀. *D. T. R.* St. John, West Indies "Antares"

1 ♂, 1 ♀ (+ 4 indet.). *B. M. (N. H.).* Barbadoes. Beekford.

1 ♀. *B O. C. 97.* Colon (in French Canal), Canal Zone. February 10, 1934. Mr. M. B. Bishop.

29 ♂, 23 ♀. *P. M. N. H.* Sabanilla, Colombia. Shore, March 16-24, 1884. "Albatross."

1 ♀. *M. C. Z.* Magdalena River, Colombia (in lagoon 100 miles from the sea). May 31, 1873. Smith.

ATLANTIC SOUTH AMERICA

2 ♂, 3 ♀. *B. O. C. 316.* Brazil (Sao Luiz do Maranhao (?)]. Dr. R. Von Ihering.

2 ♂, 4 ♀. *N. M. W.* Bahia. "Saida."

3 ♂, 2 ♀. *U. Z. M. C.* Rio de Janeiro, Brazil. Kröyer.

Form C

ATLANTIC SOUTH AMERICA

1 ♀. *Z. S. S. M.* Pernambuco. Fischmarkt. Prinzessin Therese.

1 ♂, 1 ♀. *Z. S. S. M.* Santos. April, 1932. Krieg.

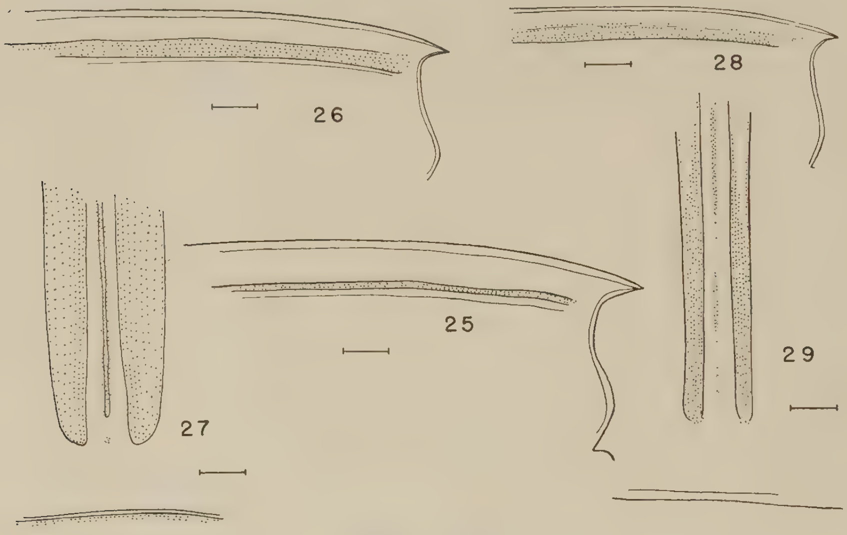
2 ♀. *Z. S. S. M.* Rio de Janeiro. Essendorfer.

1 ♂, 2 ♀. *N. M. W.* Rio de Janeiro. "Novara."

1 ♀. *B. O. C. 317* Rio de Janeiro, Brazil. Market (?); May (?). Dr. C. Moreira, through Mr. M. W. Feingold.

1 ♂, 2 ♀. *P. M. N. H. 161.* **Rio de Janeiro.**
9 ♂, 13 ♀. *M. C. Z.* **Rio Grande [do Sul (?)], Brazil. Harrington.**
1 ♂, 2 ♀. *B. M. (N. H.).* **Rio Grande (do Sul (?)]. Von Ihering.**
1 ♂, 2 ♀. *I. Z. M. U. T.* **Montevideo.**

Largest female, from off Louisiana in 70 fathoms ("Form A") carapace 53 mm., total length 201 mm.; largest male, off Louisiana in 46 fathoms, carapace 39 mm., total 179 mm. Holotype female, "Form A," carapace 11.2 mm.



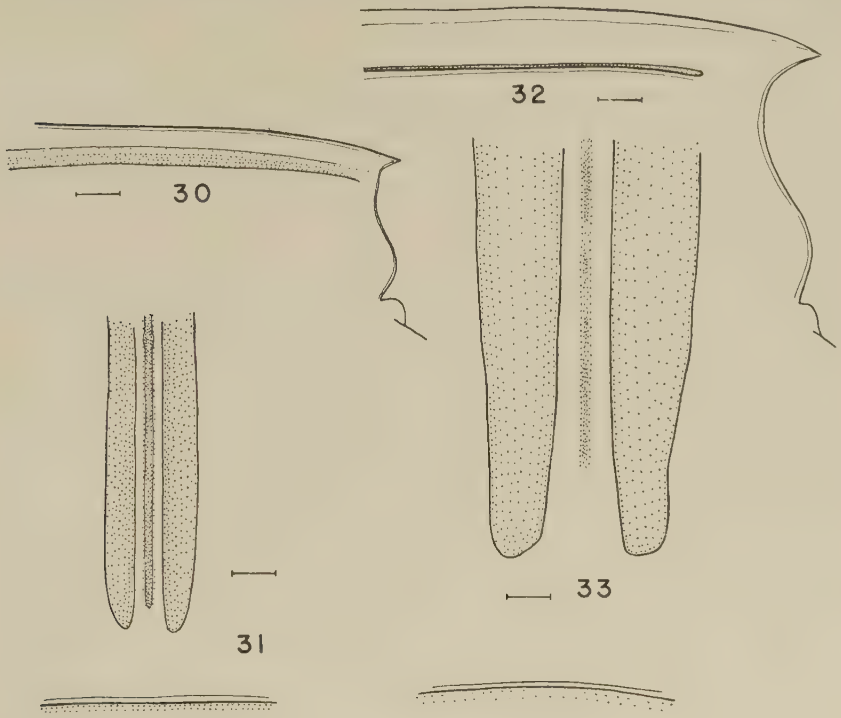
Figures 25–29

P. duorarum, n. sp., Form A. **25.** Sixth pleonic somite (posterodorsal part in lateral view); ♀ of car. 29 mm. (Pensacola, *B. O. C.* No. 303), × 6.
P. duorarum, n. sp., Form B. **26.** Sixth pleonic somite; ♀ of car. 24 mm. (Havana, *B. O. C.* No. 298), × 6. **27.** Carapace (posterior part, dorsal view); as 26, × 6.
P. aztecus Ives (restr.), Form B. **28.** Sixth pleonic somite; ♀ of car. 22 mm. (Rio de Janeiro, Un. Zool. Mus. Copenhagen), × 6. **29.** Carapace; as 28, × 6. Length of 1 mm. indicated at each drawing.

Largest male and female of "Form B," from [northern ?] Brazil, respectively 26.5 mm. and 20 mm. in carapace length. Largest male and female of "Form C," from Rio de Janeiro, Brazil, 30 mm. and 46 mm.

Smallest impregnated female of carapace 30 mm. ("Form A"). Smallest males with joined petasmal endopods, 17 mm. ("Form B")—23 mm. ("Form A").

Diagnosis: Posteromedian elevation of the median plate of adult and subadult females with a median posterior protrusion or carina which divides into a pair of divergent ridges extending anterolaterally along the edges of the elevation. These ridges often converge again anteriorly, so that the posteromedian elevation of XIII often has, in ventral view, the appearance of a diamond-shaped "prominence with a concave ventral surface."[1] Lateral plates of sternite XIV in adult females not produced anteromedially to meet in the midline, but



Figures 30–33

P. aztecus Ives (restr.), Form A. **30.** Sixth pleonic somite (posterodorsal part, lateral view); ♀ of car. 26.5 mm. (Louisiana, *B. O. C.* No. 260), × 5.7. **31.** Carapace (posterior part, dorsal view); as 30, × 5.7.

P. aztecus Ives (restr.), Form C. **32.** Sixth pleonic somite; ♀ of car. 46 mm. (Rio de Janeiro; *B. O. C.* No. 317), × 5.7. **33.** Carapace; as 32, × 5.7. Length of 1 mm. indicated at each drawing.

---

[1] The precise outline varies, however, from a very elongate figure to a broad ellipse; the relative height of the ridges varies, so that the surface which they enclose may be merely plane rather than depressed below them; the enclosed surface may occasionally bear a median longitudinal carina anteriorly, which very rarely continues back to the point of divergence of the boundary ridges; the extent of the boundary ridges anteriorly from their point of divergence varies, as well as the size of the median ridge posterior to the point of divergence. At carapace lengths below 24 mm., the posteromedian carina may appear as a simple ridge without bifurcation.

instead separated by the posteromedian elevation of XIII which is thus prominently exposed to view; ventral surface of the lateral plates not pubescent.

Medially curved distal ends of the distoventral lobes of the petasma not projecting free of the membraneous distolateral lobe; external edge of the distoventral lobes unarmed although one or two spinules may straggle out to project from the distal end; median or attached edge of the distoventral lobes, on the anterior side, with several compact series of short, crowded spines massed near the distal ends of the lobes. The fold of the free margin of the distolateral lobe, just median to the end of the distoventral lobe, projects posteriorly as a rather fleshy flap bearing a moderate spinous armature. The appendix masculina of the male second pleopods has a more or less straight, or only slightly concave, external margin.

In the typical *P. aztecus* of "Form A" [the North American and Bermudian specimens (except that from Key Largo and the one in the British Museum which, since collected by Yarrell, presumably comes from Cape Lookout); and one of several Cuban specimens of the species], the adrostral sulci of the carapace are well defined posteriorly and are distinctly broader than the carina between them; the median carina is distinctly and continuously sulcate, and the dorsolateral sulci of the sixth pleonic somite are broadly open, their breadth being from three-fourths to equal the interval between their dorsal lip and the midline (measured at a point about one-third before the posterior end of the segment).[1] The third legs are modally rather long, extending about a dactyl beyond the antennular peduncle; they range from even with the peduncle to as much as a tenth of the carpus beyond, the greatest relative lengths occurring only in the largest specimens. In specimens from Pernambuco and Santos, part of those from Rio de Janeiro, and those from Rio Grande, Brazil, comprising "Form C," the sulci of the sixth pleonic somite are extremely narrow (their width less than a third of the interval between their dorsal lip and the midline) and are sometimes entirely closed. The adrostral sulci are much as in the northern form, but the median sulcus of the postrostral carina is very shallow, and the excavated sections of it frequently are separated by plane, unsulcated intervals. The posteromedian elevation of XIII in females seems to tend to be more elongate and slender than is usual in "Form A," though it is variable in shape. The third legs do not reach beyond the antennular peduncle. Specimens from Sao Luiz (?), Bahia, and Rio de Janeiro in Brazil, from the Caribbean, the majority of those from Cuba, and from Key Largo in southern Florida, and possibly from Cape Lookout, comprising "Form B," differ from other material from Brazil and North America in that the adrostral sulci are narrower, usually much narrower than the median carina, and tend to be very ill-defined posteriorly; the sulci of the sixth pleonic somite, although narrower than in the northern "Form

---

[1] The sulci of the sixth pelonic somite were unfortunately not examined in the types, from Vera Cruz, but it seems probable that these are of "Form A."

A," range up to one-half as broad as the interval between their dorsal lip and the midline, and the dorsal lip is frequently low and ill-defined. The posteromedian elevation of XIII in females tends to be more broad and oval than in Forms "A" and "C." The modal length of the third legs seems to be about midway between that of the south Brazilian specimens and North American ones.

REMARKS: *Penaeus aztecus* most nearly resembles the Pacific American *P. brevirostris* Kingsley (Burkenroad, 1938a) and like it is distinguished from all of the other American forms by the bifurcation of the carina of the posteromedian elevation of the median plate of adult females; and also by the fact that in some individuals of either species the adrostral sulci may be very narrow and posteriorly ill-defined, and the sulcus of the postrostral carina shallow and discontinuous. It is interesting that the chiefly Caribbean "Form B" of *Penaeus aztecus* comprises those individuals which most nearly approach the narrowly sulcate extreme variants of *P. brevirostris*, both geographically and in structure. *P. aztecus* is, however, quite distinct from *P. brevirostris;* especially as regards its supra-antennal and supraorbital carinae which resembles those of the other American species in being respectively longer and sharper than in *P. brevirostris;* the absence of pubescence from the lateral plates of its thelycum; the greater length of the distomedian lobes of its petasma, the more extensive posterior protrusion and armature of the fold of the distolateral lobe of its petasma; the infrequent occurrence in only very weak spinules on the distal end of the distoventral lobe of its petasma; and the triangular or weakly falcate rather than conspicuously curved form of its appendix masculina.

The thelycum of juvenile females of *P. aztecus*, at carapace lengths between 24 and 11 mm., is sometimes difficult to distinguish from that of *P. duorarum* since at these small sizes the carina of the posteromedian elevation of XIII in *P. aztecus* may be no more than a short ridge not continued into a pair of divergent arms anteriorly. In females of *P. aztecus* of carapace less than 11 mm. the ridge is never continued anteriorly and may disappear altogether. The distinction of juvenile females of *P. aztecus* from *P. duorarum* (and also of juvenile males of *P. aztecus* from *P. brasiliensis*) therefore depends upon regionally variable differences between the forms in shape of the sulci of the carapace and sixth pleonic somite.

DISTRIBUTION: According to the available records of the three Atlantic species of the *Penaeus brasiliensis* group, there are quite considerable differences in distribution between the different forms. In particular, the material is perhaps sufficient to establish the presence of *P. duorarum* alone of the three in Africa, and the absence of this species from Brazil and Louisiana; the presence of *P. aztecus* alone north of Cape Hatteras, south of Rio de Janeiro, and in Louisiana, its absence from Haiti, southwestern Florida and Bermuda; the absence of *P. brasiliensis* from the northeastern Gulf of Mexico. The points of origin of the material available for critical determination are roughly indicated in figure 34.

An attempt to correlate the apparent differences in distribution with geographical differences in salinity or temperature has not met with very much success, as the succeeding paragraphs will show. Before entering into the description of this attempt, some points affecting the interpretation of the data at hand may be made clear. In the first place, no very complete information is readily available as to the temperature and especially the salinity of the shallow waters to which adults and juveniles of the group are limited; for example, the records from Sabanilla, Colombia, probably refer to estuarine water of low salinity at the mouth of the Magdalena River, and not to a salinity greater than 37.25°/oo such as is indicated for the surface of the neighboring waters during March by Böhnecke, 1936. Even the salinity of the neighboring off-shore waters is very doubtful or is unknown in many important regions for part or all of the year; and aside from sometimes disturbing conflicts between informa-

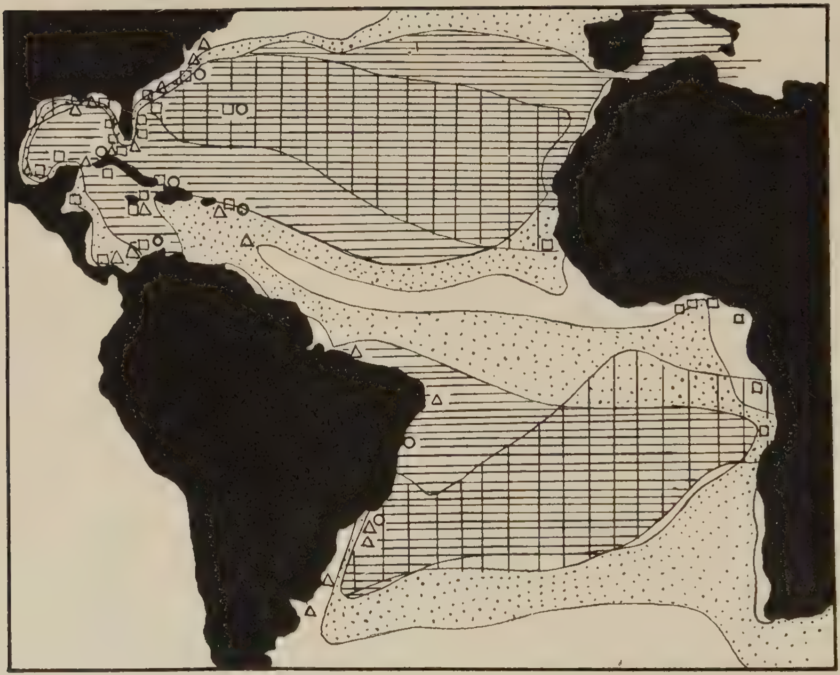


Figure. 34. Distribution of available records of Atlantic species of the *Penaeus brasiliensis* group. Circles = *P. brasiliensis;* squares = *P. duorarum;* triangles = *P. aztecus.* Horizontal bars = surface salinity > 36°/oo; stipple = surface salinity 35–36°/oo; blank = surface salinity < 35°/oo. Vertical bars = annual mean surface temperature 20°–25° C. Temperatures and salinities after Schott, 1926.

tion for the same area and season derived from different authors, such other types of difficulty might be cited as that of understanding the position at which the 36°/oo isohaline reaches the African littoral (the annual mean position being shown as south of 20° N. lat. in Böhnecke's B. XXVII, but as north of 20° N. lat. in all four of his three-month means). In the second place, the habitats of larva, juvenile and adult are quite distinct in *P. aztecus* at least (*vide* pp. 45, 51) and possibly in all of the *P. brasiliensis* group, and it seems quite probable that these differences relate to different optima or ranges of tolerance of salinity and temperature in the different stages. Since all of the stages seem to be capable of considerable movement, it is thus possible for a geographical region unsuited to the maintenance of a complete, permanent population to possess a partial or a temporary population, as in New Jersey where (*vide* p. 50) juveniles only of *P. aztecus* seem to occur, and during the warm months only. Except for a few regions, most of the available records are based on small single or uniseasonal samples of one stage only; and thus for example even if some positive idea could be formed of the environment concerned no very useful inference could be drawn from the fact that *P. aztecus* is recorded both from Sabanilla and from Rio de Janeiro, since material from the former region is juvenile, from the latter sub-adult or adult, and since the assumption that other stages of the species would occur in the same geographical area is not certainly permissible. In the third place, the number of records available, small enough in relation to the enormous distances over which they are scattered, is in effect still further reduced by the morphological subdivision of *P. aztecus* and *P. duorarum*, since there is no reason why these structurally distinguishable forms, which occupy distinct geographical ranges, should not differ from one another in physiological modes as well. By reason of the paucity of material, the species have been treated as units in subsequent paragraphs, but there is no reason, for example, to believe that *P. aztecus* Form B may not have higher thermal and saline optima than Forms A and C.

Bearing in mind the meagerness of the evidence and the uncertainties of interpretation outlined above, the distribution of records of the Atlantic species of the *P. brasiliensis* group may be examined in relation to the distribution of temperatures as shown by Böhnecke, 1936. It would appear that the extreme limits of range of the group as a whole coincide more or less closely with the positions of the annual mean surface isotherm of 20° C. (or of the maximum positions of the 25° isotherm). *P. aztecus* is recorded from beyond this limit both in North and in South America; indeed (assuming that the well-known record of "*P. brasiliensis*" from Martha's Vineyard refers to this species) it ranges at both extremes even beyond the maximum position of the 20° isotherm; but there is reason to believe that records of this species from north of Cape Hatteras at least refer to transient individuals in the warmer months. It is clear that the species do not always range, even as transients, as far as do the 20° isotherms, since *P. duorarum* is not known from north of Cape Blanco. On the other hand, all of the species are clearly indicated to be regular inhabitants of areas lying outside of the minimum extent of the 20° surface isotherms. It would seem that adults of *P. aztecus* in Louisiana are inhabitants of bottom water rarely reaching a temperature as high as 20°.

The available evidence is not incompatible with the possibility that a temperature higher than 20° C. during some part of the year may be necessary for the maintenance of a self-contained population of the species of the *P. brasiliensis* group. But that the differences in distribution between the species within extreme limits imposed by temperature can be related to differences in temperature seems much more unlikely. Thus *P. duorarum* occurs, in Africa and in Bermuda, beyond the minimum position of the 20° isotherm and the mean of the 25° isotherm, and in the Antilles within the minimum position of the 25° isotherm; consequently it is difficult, in such an undetailed view as the scarcity of data requires, to see any relation to temperature in the absence of this species from Louisiana and Brazil. In the same way the occurrence of *P. aztecus* both within the area of temperature permanently higher than 25° and beyond the position of the 25° mean seems to exclude temperature as the affect responsible for the absence of this form from Haiti, southwestern Florida, and Bermuda; and the same may be said of the absence of *P. brasiliensis* from the northeastern Gulf.

The relation of distribution to salinity at first glance appears to suggest an explanation for the differences between the species, such as temperature can hardly provide according to the preceding paragraphs. Thus, it is immediately obvious that the regions (Haiti, southwestern Florida, Bermuda) from which *P. aztecus* is certainly absent are of much higher salinity than those (Louisiana, Atlantic United States between Capes Canaveral and Hatteras, Brazil south of Cape Frio) in which complete and permanent populations of this species may be with considerable probability be assumed to be present. *P. aztecus* occurs in all twelve of the areas in Atlantic America from which members of the group are available, in which the general surface salinities are indicated to fall below 35.75°/₀₀ at some time of the year; whereas the species is known only from six of the thirteen such areas in which the general salinities are indicated not to fall below 35.75°/₀₀. In incomplete but still effective contrast to *P. aztecus*, *P. brasiliensis* seems to occur most conspicuously in the areas of highest salinity; thus it is only in the southeastern portion of the Gulf of Mexico that the minimum salinities are indicated by the various available sources never to fall below 36°/₀₀, and it is only from this region of the Gulf that *P. brasiliensis* has been recorded (together, however, with *P. aztecus*); the species is dominant (and *P. aztecus* is absent) at Bermuda, where the salinity seems constantly of the order of 36.50°/₀₀. In central Brazil, where the coastal salinities are the highest in America, both *P. brasiliensis* and *P. aztecus* occur; but it is not impossible that at, for example, Bahia, the presence of the latter is referable to a local availability of river discharge. Other areas (Rio de Janeiro, St. Croix and St. Thomas, Sabanilla, Haiti, Cape Hatteras) from which *P. brasiliensis* has been recorded, from all of which except Haiti *P. aztecus* is also known, are not clearly distinguished by salinity constantly at the highest level; but on the whole, it is perhaps possible to say that *P. brasiliensis* is dominantly found in the areas of higher, *P. aztecus* in the areas of lower salinity. It is perhaps worth note that the distribution of the Pacific-American *P. brevirostris* and *P. californiensis*, respectively most closely related to *P. aztecus* and to *P. brasiliensis*, seems to conform to what might be expected if salinity is a significant affect of the distributions of these species; since *P. brevirostris* is found to the south where, after Schott, 1935, the salinities are on the whole lower than in the north where *P. californiensis* finds its center. Inasmuch as *P. aztecus* occurs in areas of lower temperature than those most frequented by *P. brasiliensis* (although the reverse seems not to be true), it is of interest as strengthening the suggestion that temperature within the critical minima plays little part in determining differences in distribution of the species, to observe that the Pacific congener of *P. aztecus* occurs at temperatures which seem on the whole higher than those of the area in which the Pacific congener of *P. brasiliensis* is centered; the distribution of equivalent forms in the two oceans is thus reversed in relation to temperature, whereas the relation to salinity is the same.

So far, the conception of differences in response to salinity as prime determiners of the differences in distribution of members of the *P. brasiliensis* group is perhaps acceptable; although certain possible difficulties of detail have not received sufficient emphasis. But upon examination of the distribution of *P. duorarum*, this acceptability disappears; since this species, although it occurs in the high salinities of Bermuda, Yucatan and Haiti and in the lower ones of northwestern Florida and the Gulf of Honduras, is not included at all in the relatively quite extensive samples from Brazil. A still greater difficulty appears in the fact that, while the relative abundance of *P. duorarum* in the northern Gulf of Mexico seems most obviously to increase as does the salinity (the species being the only one present at Sanibel and Englewood, less abundant than *P. aztecus* at Pensacola, and completely replaced by the latter in the low salinities of Louisiana), the species occurs at very low salinities, in physical environments seemingly not greatly different from those off the Mississippi River, through the major part of its African range.

An hypothesis capable of reconciling the evidence apparently for with the evidence apparently against the control of distribution by salinity in the *P. brasiliensis* group is perhaps too easy to construct in the almost complete absence of really decisive information. Such an hypothesis might, however, have some value as a target for future investigation, and may therefore be offered. The species of the *P. brasiliensis* group are extremely similar one to another (as clearly demonstrated by the fact that they have not until the present been distinguished); and so far as random observations, made before it was realized that more than one species existed, can serve to show, their habits are not very different; they therefore seem eminently suitable forms between which to assume that effective competition may occur. It might then be considered that while the range of tolerance of salinity is very wide in all three species, the optimum salinity for *P. aztecus* is low, that for *P. brasiliensis* is high, and that for *P. duorarum* undecided or intermediate. Allowing effective competition, the unique or dominant occurrence of one of the species at its optimum salinity might thus be thought to refer not to a lack of tolerance for this salinity on the part of the other species but to their inability to compete at this salinity with the species whose optimum it represents. If it should further be assumed that *P. aztecus*, the species with the lowest optimum, is the one least able to traverse the Atlantic (by reason of an inability to utilize the oceanic islands, as Bermuda, for stepping stones), then the explanation of the occurrence of *P. duorarum* off the Congo and the Niger but not off the Mississippi might refer to the presence of *P. aztecus* in the last of these areas alone. The apparent absence of *P. duorarum* from Brazil remains a difficult question, but it might be considered that in a large part of the more northern regions of America in which *P. duorarum* occurs or prevails the distributions of the extremes of salinity seem much more limited, shifting and broken than in Brazil, and the extent and continuity of the areas intermediate or undecided in salinity much greater than in the latter region. In these circumstances, Brazil might be better adapted than for example the Caribbean to the production of populations of *P. brasiliensis* and *P. aztecus* so dense and permanent as themselves to spread into the rather limited areas between their respective optima, to the exclusion of *P. duorarum*.

Nothing has been said in the paragraphs relating to salinity as to the differing requirements of different stages of the same species, referred to at the beginning of this section. It is shown on p. 45 that while the juveniles of *P. aztecus* live in estuarine and littoral waters of Louisiana of very low salinity, the adults are more or less limited to off-shore waters of salinity 36°/₀₀ or above. It therefore seems possible that the apparently low optimum salinity for this species refers to juvenile requirements. In contrast, although juveniles of *P. brasiliensis* have been taken with those of *P. aztecus* in presumably estuarine conditions at Sabanilla, it seems questionable whether any very extensive brackish nurseries can be available for this species in the coral regions in which it is most frequent; and it might be thought that neither this species nor *P. duorarum* requires, though both may, to differing extents, tolerate water of low salinity in juvenile stages.

In the paragraph above which presents the hypothesis of limitation of distribution of members of the *P. brasiliensis* group by interspecific competition rather than by stenohalinity direct, it has been implied that *P. duorarum* has traversed the Atlantic from America to Africa rather than in the opposite direction. The opposed conception is certainly not to be disposed of in so hasty a manner, in view of the apparently greater facility of transport by the Equatorial than by the Gulf Streams; another item in its support is provided by the identity of the African with the Antillean rather than with the North American and Bermudian form of the species which might have been expected to reach Africa if transport had been by the west-east current; and it is also tempting to consider that the absence of *P. duorarum* from Pacific America relates to its arrival in the western Atlantic after the final closure of the transcontinental channels. But against these contentions is the fact that the *P. brasiliensis* group, which is very homogeneous and has no very nearly related congeners, includes five American species of which only *P. duorarum* extends to other coasts; this would certainly suggest an American origin for the group, although it leaves open the possibility that *P. duorarum* has originated in Africa from stock drifted from the west by a rare chance, and has subsequently established and maintained identity with an American colony by means of the more rapid transport offered by the Equatorial currents. This latter view would seem conciliable with all hypothetical requirements.

NATURAL HISTORY:[1] Attention has been called by Burkenroad, 1934a, p. 90, to the fact that while on the Louisiana coast small and immature specimens only of "*P. brasiliensis*" (cf. Viosca, 1920, p. 108) of a brownish color and showing little sexual difference in size or number, occur in the shallower waters, a catch of large, sexually active individuals, of an orange color and including a larger proportion of females the maximum size of which was much greater than that of the males, had been obtained from farther off-shore. Although it is not now certain that occasional individuals of *P. duorarum* may not have been included in the shallow-water material previously examined, it is possible to say that the great majority at least of specimens of the Division taken in shallow water in Louisiana (and all which have been taken off-shore) are referable to *P. aztecus;* and therefore, that specific differences are not involved in the previously described differentiation of the deep- and the shallow-water populations. The composition of the present deep-water catches agrees very well with that of the former one and like it suggests that the distinctive character of the sex-ratio of the off-shore population may be the result of a difference in longevity between males and females producing its effect in the course of several years; as will be discussed in detail below.

---

[1] In a recent paper (P. Z. S. London, 1938, II, 10, pp. 163–185) on *Penaeus plebejus* Hess, Dr. W. J. Dakin indicates the habits of this species to be in several respects somewhat similar to what has been stated for the related American form *P. aztecus* (*P. "brasiliensis"*) by Burkenroad, 1934a, p. 90. In connection with Dakin's account of the development of *P. plebejus*, attention may perhaps be called to the summary of various features of peneid development by Burkenroad (1934a, pp. 116–120 and 135–137; and 1934b, p. 9), as well as to the application (1934a, p. 76, and 1934b, p. 15) of the term SICYONINE stage to the several instars intervening between the mysis stage and the assumption of adult form in Penaeinae [in which as Dakin very justly observes (*l. c.* p. 180) "it is scarcely possible to regard the first post-mysis stages as post-larval"]. The possibility may be noted that, according to Dakin's figure of mysis and post-mysis larvae (*l. c.*), his material may have included more than one species.

From the sum of the specimens listed on preceding pages as available for systematic study of the *P. brasiliensis* group, it will be noticed that, excluding the deep-water catches of *P. aztecus* off Louisiana in 1937, the proportion of the sexes is approximately 0.9♂/1.0♀. On the other hand, in the catches of *P. aztecus* from Louisiana in March and April, 1937 (which are the only extensive ones listed from water deeper than 10 fathoms), the ratio of males to females is about ½; the twelve fruitful hauls, in from 50 to 70 fathoms having yielded 34 males to 101 females; and the eight fruitful hauls in from 12 to 50 fathoms having yielded 63 males to 89 females. The off-shore catch mentioned by Burkenroad, 1934a, consisted of 23 males and 54 females taken in about 16 fathoms in August, 1930. According to notes on catches made in Louisiana in 1930 and 1931 in less than 10 fathoms (from which the previous statements as to in-shore sex-ratio are derived), twelve fruitful hauls yielded 182 males to 199 females (a result in close agreement with that shown by the present lists of systematic material).

In hauls from 50 to 70 fathoms, the minimum and maximum carapace lengths in males are respectively 30 mm. and 39 mm., in females 34 mm. and 53 mm.; from 12 to 50 fathoms the extremes are respectively 23 mm. and 38 mm., 24 mm. and 50 mm.; in less than 10 fathoms the maximum carapace length noted for males was evidently (according to the total lengths recorded) about 25 mm., for females about 26 mm.,[1] clearly below the minimum at depths of 50 to 70 fathoms. Females from less than 10 fathoms are very rarely impregnated; from 10 to 20 fathoms the larger females are frequently impregnated; beyond 20 fathoms (where the minimum size of females rises to 30 mm.) all but a single one of the available specimens are impregnated.

It might be thought that the reduction with depth in proportion of males to females in the Louisiana catches of *P. aztecus* (roughly from .9/1 at < 10 fathoms, to 1/2 at 10–50 fathoms, to 1/3 at 50–70 fathoms) is the result of governance of movement by size (the males, as smaller than the females, remaining in shallower water). However, the adoption of this view is made difficult by the fact that the modal size of males at the greater depths is less than that of the females at more moderate ones; as well as by the probability that almost all of the males at depths of less than 10 fathoms are not fully matured, are therefore presumably similar to the females of the same area in age as well as in size, and consequently cannot be equivalent to the mature off-shore females. It therefore seems more probable that the proportion of males is progressively reduced by longer life in the females, as the locality sampled becomes progressively more remote from the littoral source of supply of approximately equal numbers of both sexes. Although the great disparity between maximum size in males (39 mm. carapace length) and that in females (53 mm.) may result from a sexual difference in rate of growth such as seems already to be foreshadowed by a small difference in size at first maturity, it is on the other hand possible that their greater size as well as their greater number might well be in part at least the correlate of a longer adult life in females.[1] Of interest in this connection is the fact that in

---

[1] In available catches of *P. aztecus* from 5 fathoms in Pensacola Bay in March the maximum is somewhat greater than that indicated in notes made in 1930 and 1931 on Louisiana shallow-water material taken throughout the range of seasons, being 32.5 mm. in females, 29.5 mm. in males. None of the Pensacola females, whether from March or September, is impregnated; and the ovaries are very immature.

---

[1] Heldt, 1932, finds (p. 6) that among approximately 600 specimens of *Penaeus trisulcatus* Leach of 22 samples taken throughout the year at Tunis, the males are the more numerous sex at the smaller sizes represented, the females at the larger. Since "Les courbes relatives aux males et aux femelles ont une correspondence remarquable, meme allure, et on pourrait presque les amener en coincidence par un simple changement d'axe des *y* pour l'une d'elle," Heldt concludes (p. 7) that "Cette difference de tailles tient plutot à une croissance plus rapide des femelles qu'à un age moindre des males."

From Heldt's Graph 3, p. 8, it appears that there are 53 ♂ to 170 ♀ at total lengths of 145 mm. or above, the maximum in males being 178 mm., in females 203 mm. Both the maximum sizes and the sex-ratio among the larger specimens thus resemble those in *P. aztecus*, where females preponderate after the inception of sexual activity at about 145 mm. (= 30 mm. carapace length). But whereas in American material of less than 145 mm. in length the two sexes are immature and are approximately equal in number, Heldt (p. 4, p. 7) considers that her entire material is adult and can "peuvent devenir aptes à la reproduction" at the minimum sizes represented; and finds that among her specimens of less than 145 mm. (the minimum length of the males being 96 mm., of the females 107 mm.) there are 227 ♂ to 121 ♀. It is such a preponderance among *adults* of males at the smaller sizes, which [together with the indication in Heldt's Table I, p. 5, that the mean size of the females is above that of the males (by an average of 15 mm., modally 10–20 mm.) in every sample (over a range in mean length of females in the various samples from 125.4 to 188.4 mm.)] would provide the best support of Heldt's conclusion that the relative infrequency of males at the larger sizes is the result of less rapid growth rather than of shorter life; since it seems not impossible that the "correspondence remarquable" in shape of the length-frequency curves of the two sexes might be referable to the effects in combination of the correlation suggested by Heldt's Table 1, p. 5, between number of males and of females per sample (over a range in content of sample from 7 to 115 individuals) and that in size between males and females of each sample.

But unless the smaller specimens dealt with by Heldt are, as she believes, adult, it would be necessary to show either that at sizes below that at which the females become mature the greater abundance of males is commensurate with the number of sexually active individuals included among them, or else that maturity occurs at a

P. setiferus, where there does not appear to be quite so strikingly low a proportion of adult males as in *P. aztecus*, the males also attain a relatively greater maximum and adult mean size than in the latter.

The largest off-shore females are nearly twice as long in carapace and nearly three times as heavy as the inshore maximum. According to available material from Louisiana, impregnation, and ripening of the ovary, occur only in depths greater than 10 fathoms, first appearing at carapace lengths of about 30 mm., that is slightly (or not at all) above the inshore maximum. Since all females taken at depths of 20 fathoms or more have attained sexual maturity (as indicated by the impregnation of all but one, ripeness of the ovary in many of all sizes), it may be argued that the range of size in these sexually mature females, from 30 to 53 mm., can hardly represent individual variation in size at time of maturation (although it is of course within possibility that, since impregnation seems to have no close relation to imminence of spawning, those small impregnated females with unripe ovaries might not spawn for the first time until they had attained much larger sizes). In any case, however, it can definitely be stated that the inshore nursery of the species does not supply any females within 20 mm. of the maximum carapace length attained in the off-shore stock of the same sex. If it is a permissible assumption that the time involved in an increase in carapace length of the individual from 30 to 53 mm. is as great as that required for development from metamorphosis to a carapace length of 30 mm. (and this is certainly a conservative estimate, since the rate of linear growth might reasonably be expected to diminish at the larger sizes, and with the assumption of egg-production on the scale characterizing the species), then it would seem that the maximum length of life in females of *P. aztecus* is at least double the period spent in inshore waters, probably much more.

Assuming that the females of maximum size first spawned at sizes little above 30 mm., it would seem that these individuals must have a lifetime including more than one, perhaps several, spawnings. Non-histological examination of the ovary (by sampling the section lying within the anterior part of the pleon) reveals nothing at variance with this assumption. In the inshore females the

---

greater age in the males than in the females, before it could be thought certain that the greater abundance of males than of females at a given small size is a consequence of the greater age attained by the former before passing these dimensions. It is therefore interesting to remark that in the single available sample of *P. trisulcatus* (B. O. C. 19, purchased in the market at Port Said by Mr. Richard Colestock in March, 1932) which as it happens does not agree in sex ratio with that found by Heldt among her smaller specimens [since it consists of 58 males (of maximum size 99 mm., minimum 76 mm.) and 76 females (of maximum size 104 mm., minimum 74 mm.)], all of the individuals (including those which approach or exceed the minimum size in Heldt's material) seem very far from readiness for reproductive activity, and the specimens indeed recall in sexual state those of *P. aztecus* of similar size.

ovary is small and compact, and its lobules are crammed with minute transparent cells. Among the 183 off-shore (depths $>$ 20 fathoms) females examined, the ovary is ripe in 45 [large; densely crammed with opaquely yolky, yellow eggs of columnar structure which measured along the surface of the ovary average in the various individuals from 4 to 5 to the millimetre (probably equal to a somewhat smaller mean spherical diameter)]. In 82 off-shore specimens the ovary is ripening, its cortex crammed with more or less heavily granular eggs ranging in mean size from 5.5 down to about 10 per mm. In about 44 specimens, the ovary is quite undeveloped; in most of these its lobules are subdivided into more or less well-defined follicular pouches associated with very young ova; rarely, the appearance is similar to that in inshore females where the follicular appearance is not marked and the ova not well developed. Finally, the ovarian condition of 12 of the specimens differs from that in the others which seem to form a simple series of ripening stages. In 9 of these 12, the lobules of the ovary are subdivided into well-defined thick-walled follicular pouches, but there are no clearly-differentiated young eggs. In 2 of these 9, some few large ripe eggs with columnar cortex are present among the thick-walled follicular pouches; and it would therefore seem possible that in these specimens the ovary has recently been (not quite completely) emptied. In the remaining 3 of the 12 specimens, the follicles are associated with more or less well-developed young ova, but a few large, ripe, yolk-laden eggs are also present; these might simply be cells which have outstripped their neighbors in development, but it would seem possible that they are eggs not discharged at a previous spawning, as in the 2 specimens with some ripe eggs among the empty follicular pouches. If this interpretation is correct, it would appear that, as suggested by other evidence, spawning in *Penaeus aztecus* is followed by redevelopment of the ovary toward another spawning.

According to the frequencies of spawned-out, undeveloped, ripening, and ripe ovaries in the March and April off-shore catches of *P. aztecus*, the spawning-season of this species in the Gulf of Mexico would seem at best ill-defined; and in conformity with this conjecture, notes made in 1930 indicate that females of carapace 40–45 mm. taken at 16 fathoms in August and at 12 fathoms in December had well-developed ovaries. Among the March and April off-shore specimens there is some indication that ovarian condition may vary somewhat less in individuals from the same haul than it does from haul to haul; no other correlation, as with size or with depth of capture, is apparent. The very curious fact, that all available spent females are impregnated, would seem to indicate that this appearance of the ovary must persist for a time at least sufficient for molting, mating and hardening of the new skin. One soft-shelled and newly impregnated spent female was noted, but the number of spent individuals was insufficient to indicate whether a larger proportion of soft-shells than in the general population occurs, as would seem required if the immediate reimpregnation of spawned females is customary.

In general, the spermatophores give the appearance of having been most recently acquired in soft- or paper-shelled individuals, in which conspicuous rags of sperm-free material (presumably the partial equivalents of the sturdy "wings" in *P. japonicus* and *P. trisulcatus*) protrude around the meeting of the lateral with the median plates of the thelycum; and in which the floor or dorsal wall of the receptacle seems not yet to have sunk in sufficiently for easy accommodation of the spermatophores. As spermatophores are present in all but one of the females from depths greater than twenty fathoms, whether ripe or unripe; and inasmuch as the state of the ovaries in soft-shelled females indicates that molting may occur between spawnings, it would seem that copulation in *P. aztecus* takes place immediately after the molt in adult females, whether or not these are likely to spawn before the succeeding molt. That this is probably the case is indicated by a female of *P. brasiliensis* with unripe ovary 24 mm. in carapace length, in the collection of the Department of Tropical Research, New York Zoological Society. This specimen, taken in shallow water in Bermuda by Dr. Beebe, molted in an aquarium; its shed skin bears spermatophores in the sperm receptacle, the isolated soft-shelled animal being of course unimpregnated.

It is interesting to observe that in the course of semi-monthly trawlings extending throughout 1932 in a series of localities in Delaware Bay and off the Atlantic coast of southern New Jersey in depths up to 10 fathoms (made by the U. S. Bureau of Fisheries in cooperation with the Bingham Oceanographic Laboratory, under the direction of Professor A. E. Parr), *Penaeus aztecus* first appeared at the end of August at a minimum carapace length of 17 mm. in females, 13 mm. in males, and disappeared completely at the end of October when the minimum sizes obtained were 21 mm. in females, 23 mm. in males. The maximum size obtained was 34.5 mm. in females, 28 mm. in males, in September and October; the August maxima were 28 mm. in females, 22.5 mm. in males. Two of the females, of 32 mm. and 34 mm., taken in September and October, were impregnated although their ovaries presented the usual undeveloped appearance. Inasmuch as Mysid, Crangonid, and Palaemonid shrimp of sizes much smaller than the minimum of *P. aztecus* in New Jersey were regularly obtained in the trawlings, it appears probable that the young *Penaeus* had spent their earlier life in other localities than those in which they appeared in August; that these localities may have been some distance away is indicated by the fact that the New Jersey waters had reached temperatures (64°–74° F.) higher than those of October in June, two months before the appearance of *Penaeus*. At the same time, topographic and hydrographic conditions on the continental shelf off New Jersey make it seem unlikely that *Penaeus aztecus* from this area can spend the winter in neighboring deeper water. Inasmuch as fishes of the Middle Atlantic coast are known to retire southward with the approach of winter, and to move northward again in summer (Parr, 1933), it would seem possible that in *Penaeus aztecus* on the Middle Atlantic coast there is a northward dispersal of juveniles and subadults from more southern areas of spawning and metamorphosis, possibly followed by a successful return of the maturing individuals. Although data are almost lacking, it seems probable that sexually active adults of *Penaeus aztecus* occupy a range deeper than that of the immature, on the Atlantic as well as on the Gulf coast.

Although very little evidence is available, the absence of individuals of *P. duorarum* of maximum size from shallow-water collections, together with the fact that the available individuals of maximum size were taken in depths greater than 10 fathoms, seems to indicate that this species also may retire permanently to deeper water after a littoral youth.

Postmysis larvae of the Division in the sicyonine stage, elongate and transparent free-swimming animals with a red ventral stripe (of structure rather similar to but reaching a size nearly twice that of the same stage in *Penaeus setiferus;* of a size and general type somewhat similar to that of postmysis larvae figured by Kemp, 1913, fig. 36a, for "*Penaeus carinatus*," and by Gurney, 1926, fig. 57, as of "*Penaeopsis* sp.") are frequently encountered at the surface of the American seas remote from shore; as well as in shallow brackish pools far inland (e. g., on James Island, S. C., April 22, 1935, found with the aid of Mr. G. R. Lunz, Jr., of the Charleston Museum). Oceanic and littoral postmysis larvae have been determined to be of "*P. brasiliensis*" auct. by rearing, aboard "Atlantis" in 1935, and instars up to recognizable juveniles occur with the sicyonine stages in inland pools; but the postmysis larvae have not yet been distinguished as regards the species now recognized. Whether larvae of *P. duorarum* can metamorphose to juvenile in the brackish waters, or whether those of *P. aztecus* can long survive far off-shore, can therefore not be stated at present, but it would not be surprising to discover as great a divergence between the species in larval habitat as in adult distribution. That the postmysis larvae of whatever species found on the high seas can successfully metamorphose without drifting to the coast seems unlikely, since no juveniles of *P. aztecus* or of *P. duorarum* were encountered even in the moderate depths tolerable to the adults [juveniles of *P. duorarum* have been recorded by Faxon, 1896, p. 162 (as "*P. brasiliensis*") off the Tortugas in "955 fathoms," but it seems quite possible that these may have been individuals derived from the nearby banks and swimming near the surface (a common habit in juveniles and subadults of the group, *cf.* Wheeler, 1937) when captured]. Mysis and especially premysis stages of *P.* "*brasiliensis*" are very infrequently encountered in surface or shallow-water hauls by comparison with the postmysis stages, and the eggs are completely unknown; consequently it seems quite possible that the eggs of American members of the Division occur on or near to bottom in 20 fathoms and more,[1] the later larvae only normally reaching the upper layers or the littoral and estuarine waters.

---

[1] According to a letter from Dr. W. J. Dakin of the University of Sydney, his search for the early stages of *Penaeus plebejus*, an Australian member of Division II, has

yielded results comparable with the above as regards the preponderance of post-mysis stages in the upper layers, and the lack of eggs; and he agrees that the floating eggs and nauplii which he reported in 1935, p. 24, may be referable to some other genus than *Penaeus*.

Pearson, 1935, p. 172, has announced the discovery of nauplius-containing eggs .38–.42 mm. in diameter, floating at the surface in water about 5 fathoms deep off Georgia; he considers these "most probably" to be of *Penaeus setiferus* (a member of Division I), but this identification seems open to question.

The results of oviposition by specimens certainly referable to *Penaeus* in the current usage of this name have twice been recorded: According to the abstract of a paper by Huzinaga, 1935, the pale yellow eggs of an Indo-Pacific species of Division II, *Penaeus japonicus* Bate, .25 to .30 mm. in diameter, are demersal. According to Heldt, 1931, p. 1039, the eggs of the Mediterranean member of the Division, *Penaeus trisulcatus* Leach, evidently remain in suspension for a time only after spawning in aquaria, "ne tombant sur le fond qu'au bout de plusiers heures." It may be remarked, as regards the floating or sinking of eggs *in vitro*, that their specific gravity may be critically related to that of the water column in the normal spawning area (*cf.* Jacobsen and Johansen, 1908; and also Mortensen, 1897, pp. 330–31); the observations cited accordingly do not prove that the eggs of these species of *Penaeus* may not occur at the surface, but they do suggest this possibility. It is interesting to note that Heldt finds the ripe ovarian eggs of *P. trisulcatus* to range in color from whitish yellow to clear olive-green (a color not seen in *P. aztecus*). The ovarian eggs measure .25–.31 by .22–.27 mm. (evidently only very little larger than the maximum observed in *P. aztecus*); it is stated that the egg-membrane swells considerably on contact with seawater but the dimensions of the free egg are, unfortunately, not given.

It seems remotely possible that a further record of the spawning of *Penaeus trisulcatus* in captivity is supplied by Monticelli and LoBianco, 1901a, who state that the eggs of "*Penaeus membranaceus*" are similar to those of *Eusicyonia* but smaller and of a yellowish-gray color, and are not found in the plankton. The name "*Penaeus membranaceus*" would properly refer to *Parapenaeus longirostris* (since the authors concerned employ the name "*Solenocera siphonoceros*" for the other peneid to which the specific name *membranaceus* has been applied); but since the ovarian eggs of *Parapenaeus*, both in the Gulf of Mexico and in the Mediterranean (Heldt, 1932, p. 4) are bright greenish-blue in color, and since the *Parapenaeus* is a rather delicate species living at considerable depths and consequently difficult to obtain alive, some doubt as to whether Monticelli and LoBianco may not have erroneously employed this specific name for the true Mediterranean *Penaeus* is perhaps permissible.

Aside from the above reports, eggs referred to *Penaeus* are unknown. Those of some other genera have been otained not only in captivity but from the plankton; thus Monticelli and LoBianco, 1900, p. 23, find the eggs of "*Sicyonia sculpta*" [= *Eusicyonia carinata* Olivi] to be deposited on the sand but to be readily swept up by currents into the plankton; size is not given, but it is stated that the egg membrane swells considerably on contact with the sea-water; color is said to be dark green. According to the same authors, 1901b, the red-brown segmenting eggs of "*Solenocera*

PARAPENAEUS Smith

In a recent paper Ramadan (1938, p. 73) reports his inability to detect in members of the genus the pair of minute mobile spinules which is stated to occur on the telson [of the genotype] by Burkenroad (1934a, p. 107; 1934b, p. 9). As the spinules are in fact rather difficult to find, some drawings (figures 35, 36) are herewith given. Although the spinules are sometimes absent in *P. longirostris* (particularly in the largest individuals), the pair of small pits from which they originate often remains perceptible. Similar spines frequently occur in the three Indo-Pacific species of the genus available to me; usually not in the largest specimens, but nearly as often as not in adults of small to moderate size.

Parapenaeus longirostris (Lucas)

P. longirostris, Sund, 1920, p. 32; Stephensen, 1923, p. 18, part [adult]; Heldt, 1930, p. 3; 1932, p. 12; Burkenroad, 1934, p. 108; Karlovac, 1936, p. 60.

Funchalia woodwardii ?, part [larva], Stephensen, 1923, p. 26.

MATERIAL:

653 ♂, 786 ♀. *B. O. C. 279 to 293.* "Atlantis" St. 2814, 2819, 2822, 2840, 2853 No. 2, 3, 4, 5, 6, 7, 10, 11, 12, 13, 14; March 21–April 10, 1937. 18–102 fathoms.

1 ♀. *B. O. C. 278.* "Atlantis" St. 2381; 28° 35′ N., 89° 46′ W.; March 26, 1935. 96–110 fathoms.

1 ♀. *B O. C. 277.* "Atlantis" St. 2400; 27° 37′ N., 95° 50′ W.; March 31, 1935. 120–180 fathoms.

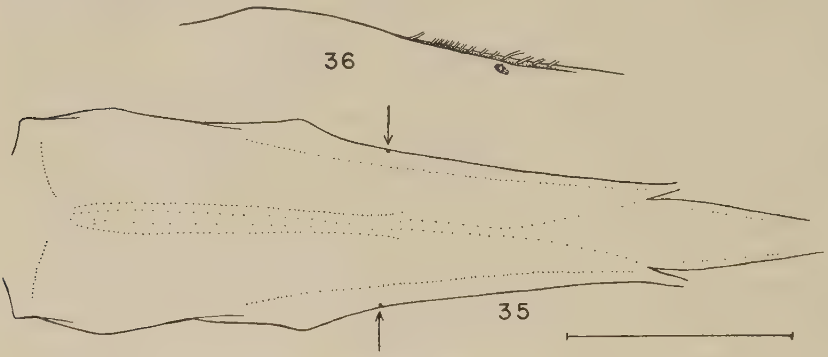
In the catches here reported upon (which however exclude the larval and most of the early juvenile material taken in the one-foot stramin net), the maximum carapace length of the males is 13.5 mm., the minimum 4.5 mm.; of the females, 24 mm. (total length 104 mm.) and 5.5 mm. The smallest male with joined petasmata was of carapace 7.5 mm.; the usual minimum for this condition was 8.5 mm.

---

siphonoceros" [= *S. membrenacea* Philippi], .32 mm. in diameter, are found floating in midwater. Gurney, 1926, p. 233, has described nauplius-containing planktonic eggs .32–.41 mm. in diameter from the lakes of the Suez Canal, together with larvae of several stages, which he is inclined to assign to *Metapenaeus stebbingi* Nobili; the larval series would at any rate seem not to have *Penaeus* as a parent. The eggs of *Acetes japonicus* (unlike those of *Lucifer* which are attached to the third legs of the female) are free-floating, according to the abstract of a paper by Soesima, 1926; as are the greenish-gray eggs of *Sergestes lucens* according to the citation by Gordon, 1935, p. 313, from Nakazawa, 1916.

On the whole, it appears likely that the eggs of the genus *Penaeus s. str.* occur in nature near or on the bottom where their discovery would be a difficult matter; since although members of this genus are by far the most abundant of the littoral peneids, ova at all reliably referred to them have so far only been obtained *in vitro*, in contrast to the planktonic catches of eggs reported for *Solenocera*, *Metapenaeus*, *Eusicyonia*, *Acetes*, and *Sergestes*.

Remarks: *Parapenaeus longirostris* is by far the most numerous species in the area investigated by "Atlantis"; and even considering the whole of the area available in the neighborhood of the Mississippi, from the brackish inside shores to or beyond the edge of the continental shelf, its numbers are probably of the same order of magnitude at least as those of *Penaeus setiferus*. But the largest catch of *Parapenaeus* (611 specimens, at St. 2853 No. 12, 30 fathoms), approximately equal in number of individuals to the largest catch of *Penaeus setiferus* (at St. 2839, 12.5 fathoms), amounts in volume only to about 1 1/3 quarts, as compared with 10 gallons of the *Penaeus*.



Figures 35–36

Parapenaeus longirostris (Lucas). **35**. Telson (dorsal view, showing diagrammatically the position of the minute pits which frequently bear mobile spinules). **36**. Telson (dorsolateral view of right margin of the middle part, showing a mobile spinule of exceptional development although with broken tip); ♀ of car. 19.5 mm. (Mediterranean, Un. Zool. Mus. Copenhagen), × 29. Length of 1 mm. indicated at each drawing.

In the Eastern Atlantic and the Mediterranean, a species of *Parapenaeus* systematically indistinguishable from that in the American North Atlantic, the Caribbean, and the Gulf of Mexico supports an important fishery. The species seems to have a range in Mediterranean waters (20–250 fathoms) not very different from that in the Gulf of Mexico; and the Mediterranean commercial fishery is conducted in about 75 fathoms (Heldt, 1930, p. 6), not much deeper than the level of great abundance in the Gulf. The European stock, however, reaches a total length of 165 mm. (Karlovac, 1936, p. 60), as compared with the recorded maximum of only 104 mm. for the west; and since the lack of American records of large individuals at any depth (together with the maturity of the small specimens available), and especially since the relation of rostral to total length in the 70–100 mm. individuals of the "Atlantis" catches [which is equivalent to that shown by Heldt (1932, p. 16) in Tunisian specimens of 120–150 mm.] indicate the western material at present available to include the maximum size in the population, it seems unlikely that the American stock is of any commercial value.

Analysis of the fifteen 1937 catches of juveniles and adults of *Parapenaeus longirostris* gives the following results: Five of seven catches between 45 and 103 fathoms were of more than 100 individuals; only one of eight catches in 18–45 fathoms was of this order of magnitude (although the one large catch at 30 fathoms far exceeded any other obtained). Between 45 and 103 fathoms, 292 males and 368 females were taken as compared with 394 males to 280 females in 18–45 fathoms; or expressed in another manner, in all of the four hauls at 60–100 fathoms there were fewer males than females, in all four at 18–30 fathoms there were more males than females. Maximum sizes of the males in hauls at more than 45 fathoms ranged from 11 mm. to 13.5 mm.; of females from 16 mm. to 24 mm.; in comparison, maximum sizes of males in hauls at 45 fathoms or less ranged from 6.5 mm. to 12.3 mm., of females from 7.5 mm. to 15 mm. The small catch at 100 fathoms included not only the largest females but proportionately the fewest males. From these figures, it would seem that a differential with increasing depth of capture in favor of the female sex and the larger size, such as has been indicated on preceding pages also to obtain in *Penaeus aztecus* (where the smaller individuals are massed in the inner littoral zone beyond the range of *Parapenaeus*) occurs in the present species.

Since many of the females of *Parapenaeus* had well developed, bright greenish-blue ovaries, and since larvae and post-larvae were abundant, it would appear that spawning must have begun at an indefinite time before the season of investigation and must continue for an indefinite period beyond it.

TRACHYPENEUS Alcock

Trachypeneus similis (Smith)

T. similis, Burkenroad, 1934a, p. 102; 1934b, pp. 50, 51; Schmitt, 1935, p. 131.

MATERIAL:

15 ♂, 37 ♀. *B. O. C. 335* to *345*. "Atlantis" St. 2828, 2830, 2838, 2840, 2853 No. 2, 3, 4, 6, 7, 12, 13. March 23–April 10, 1937. 12 to 48 fathoms.

23 ♂, 42 ♀. *B. O. C. 346* to *348*. Pensacola Bay, Florida; March 11, March 13, March 16, 1935. 5 fathoms.

3 ♀. *B. O. C. 58*. Pensacola Bay, Florida; February 22–26, 1932.

2 ♂, 6 ♀. *B. O. C. 59*. Pensacola Bay, Florida; March, 1932.

Males with joined petasmata, carapace length 7 mm. to 13.8 mm.; juveniles (Pensacola Bay) of 5.5 mm. and 7 mm. Females of carapace 8.5 mm. to 23.5 mm. The smallest impregnated female obtained has a carapace of 11 mm. In the catches from Pensacola in 1935, little more than one-fourth of the females are impregnated, and unimpregnated specimens occur throughout the total range of sizes. In the Gulf catches made in 1937, a week to a month later in the year, nearly two-thirds of the females are impregnated, and the unimpregnated specimens are limited to the lower half of the range of sizes.

Remarks: It is interesting to note that five hauls in Pensacola Bay yielded a total of 76 specimens of *T. similis* but none of *T. constrictus;* whereas two hauls in the open Gulf east of 88° 10′ W. (one just outside of Pensacola Bay, the other off Mobile) yielded 16 specimens of *Trachypeneus constrictus*, none of *T. similis*. The frequent presence of *T. similis* in the open Gulf west of 88° 10′ W. and the apparent rarity there of *T. constrictus* is therefore rather suggestive of a response to the lowering of salinity toward the west. It is extremely difficult, however, to refer the differences and similarities in distribution of *T. similis* and *T. constrictus* over their entire geographical range (*T. constrictus* alone on the Atlantic coast of the United States and in Bermuda; *T. similis* alone in the Gulf of Paria; both species in Puerto Rico) to differences in the salinity and temperature of the various regions. A more detailed knowledge of the local conditions of capture than is entered in the literature might remove some of the apparent inconsistencies; but on the other hand it is possible that the distribution of the two species is governed by other factors than those mentioned (thus, *T. similis* might be a creature primarily of muddy, *T. constrictus* of sandy bottoms).

Trachypeneus constrictus (Stimpson)

T. constrictus, Burkenroad, 1934a, p. 102; 1934b, p. 5, 5; Schmitt, 1935, p. 131.

Material:

2 ♂, 4 ♀. *B. O. C. 332.* "Atlantis" St. 2813; March 20, 1937. 19 fathoms.
2 ♂, 8 ♀. *B. O. C. 333.* Gulf of Mexico off Pensacola; March 23, 1935. 5 fathoms.

Males from 19 fathoms have carapace lengths of 13 mm. and 13.5 mm.; females of 16.8 mm. to 18 mm. Males from 5 fathoms have carapace lengths of 10 mm. and 10.5 mm., females of 12 mm. to 17 mm. Petasmata are coupled in all males. All females from 19 fathoms are impregnated; five of those from 5 fathoms are unimpregnated.

Remarks: The possible difference in color between *T. similis* and *T. constrictus* noted by Burkenroad, 1934a, p. 102, can now be confirmed; *T. similis* is conspicuously marked with orange and red, *T. constrictus* with lavender and chocolate.

XIPHOPENEUS S. I. Smith

Xiphopeneus kroyeri (Heller)

X. kroyeri, Burkenroad, 1934a, p. 103; Schmitt, 1935, p. 132.

Material:

1 ♂, 6 ♀ adult. *B. O. C. 294.* "Atlantis" St. 2853; April 9, 1937. 16–24 fathoms.

Male of carapace length 20 mm.; females of 20.5 mm. to 24 mm.

EUSICYONIA Stebbing

Eusicyonia brevirostris (Stimpson)

E. brevirostris, Burkenroad, 1934b, p. 84.

MATERIAL:

8 ♂, 8 ♀. *B. O. C. 296.* "Atlantis" St. 2913; March 20, 1937. 19 fathoms.
1 ♀. *B. O. C. 297.* "Atlantis" St 2840; March 25, 1937. 30 fathoms.
1 ♂. *B. O. C. 295.* Louisiana. Mr. P. P. Viosca, Jr.

Largest female, carapace length 37.5 mm., total 98 mm.; smallest, of carapace 11.5 mm. Male from "Louisiana," carapace 19 mm. The six adult males from St. 2813 range from 9 mm. to 16 mm.; the two juveniles from the same station, with unjoined petasmal endopods, have a carapace of 7 mm.

REMARKS: The species has not previously been recorded from the northern Gulf of Mexico.

In form of rostrum and position of dorsal carapacic teeth the present series displays the full range of variation which has been previously observed in the species.

The color in life of *E. brevirostris* is as follows: Dorsum brown; sides white; belly pink. In detail, the ventral edge of the carapace, and the antennal scales, pleopods and inner ventral edge of uropods are rose red. The telson, inner dorsal edge of uropods, pleonic sternites and middle of sides of pleon (between the dorsal brown and ventral white) are washed with pink. The dorsal teeth of the carapace, the posterior end of the dorsal ridge of each pleonic somite, and the sides of carapace and pleon are white. The dorsal ridges of carapace and pleon are chiefly mahogany, the dorsum otherwise olive-brown. The legs are banded with violet or red and white; the antennal flagella are basally mauve, deep lake in the middle, white at tip.

Eusicyonia stimpsoni [A. Milne-Edwards MS] (Bouvier)

E. stimpsoni, Burkenroad, 1934a, p. 121.
Sicyonia dorsalis, Rathbun, 1901, p. 103, part (?).
Eusicyonia edwardsii, Schmitt, 1935, fig. 6.

MATERIAL:

1 ♀, carapace length 5.6 mm. *B. O. C. 334.* "Atlantis" St. 2814; March 21, 1937. 60 fathoms; 1-foot net on trawl-wing.

REMARKS: The present is the first certain record of the species from the northern Gulf of Mexico, but it is quite probable that part or all of the material of "*Sicyonia dorsalis*" recorded by Rathbun, 1901, from "Albatross" stations 2403–2405, off Appalachicola, western Florida, in 30–88 fathoms (as well as various of the specimens from other localities attributed by the same author to the same name) refers to *E. stimpsoni*.

Comparison of the present badly battered individual with the paratypes (M. C. Z. No. 7225) from the Barbados, a male of carapace 7.3 mm. and two females of 6.8 and 8.6 mm. very kindly loaned by Dr. F. A. Chace of the Museum of Comparative Zoology, reveals no very great differences. The rostrum is shorter and not so strongly elevated in the present specimen and is distally decurved; the lateral ridge of the rostrum is not quite so close to the inferior margin and is concave ventrally; the ventral rostral tooth is not placed so far behind the two dorsal elements of the tip. In these features the present specimen thus makes some approach to its Pacific American congener *E. picta* (Faxon) (Burkenroad, 1938a), a form certainly very closely allied to the Atlantic one. As in the Barbados paratypes, however, the surface of the pleon of the present specimen is tuberculate; whereas it is smooth in Pacific specimens.

Eusicyonia dorsalis (Kingsley)

E. dorsalis, Burkenroad, 1934a, p. 121; auct., part (?).
NOT *Sicyonia dorsalis*, Verrill, 1922, p. 49.

MATERIAL:

1 ♀, carapace length 12.5 mm. ***B. O. C. 299.*** **Louisiana. Mr. P. P. Viosca, Jr.**

REMARKS: The present specimen is the fifth one definitely known to be of this species. The type, from the Tortugas, is the only critically identified specimen so far known from other regions than Louisiana. Material from shallow water in Bermuda, referred to *E. dorsalis* by previous workers, actually represents a distinct species (to be described in a forthcoming paper) nearly resembling *E. dorsalis* in the bifurcation of the distoventral projection of its petasma, but with quite different pleonic sculpture. *E. dorsalis* seems to occur at lesser depths than does the species, *E. stimpsoni* with which it has very commonly been confused.

The present specimen makes some approach to its Pacific congener *E. disdorsalis* Burkenroad (1934b, p. 96) in that the ventral tooth of the rostrum is well developed, the postero-ventral angle of the pleura of the second pleonic somite is not sharply defined, and the telson bears no trace of lateral armature. The pleon is however tuberculate, the ventral margin of the pleura of the third pleonic somite conspicuously convex, and the anterior tooth of the carapace is placed nearly half as far from the posteriormost rostral tooth as from the posterior tooth of the carapace, and about 15% of the carapace length behind the orbit.

CITATIONS

ANDREWS, E. A.:

1911. Sperm transfer in certain decapods. *Proc. U. S. National Museum*, XXXIX.

BÖHNECKE, G.:

1936. Temperatur, Salzgehalt und Dichte an der Oberfläche des Atlantischen Ozeans. *Wiss. Ergeb. Deutschen Atl. Exped. auf F. V. "Meteor,"* V, Atlas.

BURKENROAD, M. D.:

1934a. The Penaeidea of Louisiana. *Bull. American Mus. Nat. Hist.*, LXVIII, 2.

1934b. Littoral Penaeidea chiefly from the Bingham Oceanographic Collection. *Bull. Bingham Oc. Coll.*, IV, 7.

1936a. The Aristaeinae, Solenocerinae and pelagic Penaeinae of the Bingham Oceanographic Collection. *Bull. Bingham Oc. Coll.*, V, 2.

1936b. A new species of *Penaeus* from the American Atlantic. *Ann. Acad. Brasileira Sci.*, VIII, 4.

1937. Some remarks on the structure, habits and distribution of the benthonic sergestid *Sicyonella* Borradaile. *Ann. Mag. Nat. Hist.* (10), XIX.

1938. The Templeton Crocker Expedition. XIII. Penaeidae from the region of Lower California and Clarion Island. *Zoologica* (*Sci. Contr. New York Zool. Soc.*), Vol. XXIII (part 1).

DAKIN, W. J.:

1935. Science and Sea Fisheries with special reference to Australia. *Pap. Proc. Roy. Soc. Tasmania*, 1934.

DEKAY, J. E.:

1844. Crustacea. Natural History of New York, I, Zool. 6. *New York.*

EDWARDS, H. MILNE:

1837. Histoire Naturelle des Crustacés. II. *Paris.*

FAXON, W.:

1896. Reports on the results of dredging . . . by the U. S. C. S. S. "Blake." XXVII. Supplementary notes on the Crustacea. *Bull. Mus. Comp. Zool. Harvard*, XXX, 3.

GIBBES, L. R.:

1850. On the carcinological collections of the United States. *Proc. American Assoc. Adv. Sci.*, III.

GORDON, I.:

1935. On new or imperfectly known species of Crustacea Macrura. *Journ. Linn. Soc. London*, Zool., XXIX, 226.

GURNEY, R.:

1926. Zool. Res. Cambridge Exped. Suez Canal. XV. Report on the larvae of the Crustacea Decapoda. *Trans. Zool. Soc. London*, XXII.

HELDT, H.:

1930. La Crevette Rose du Large dans les Mers Tunisiennes. *Notes Stat. Oc. Salammbo*, XIV.

1931. Observations sur la ponte, la fecondation et les premiers stades du developpement de l'oeuf chez *Penaeus caramote* Risso. *C. R. Acad. Sci. Paris*, CLXLIII.

1932. Sur quelques différences sexuelles chez deux Crevettes Tunisiennes. *Bull. Stat. Oc. Salammbo*, XXVII.

HELLER, C.:

1868. Crustaceen. *Reise Ö. F. Novara um die Erde*, Zool. T., II, 1.

HERBST, J. F. W.:

1796. Versuch einer Naturgeschichte der Krabben und Krebse, II. *Berlin u. Stralsund.*

HUZINAGA, M.:

1935. Studies on the development of *Penaeus japonicus* Bate [Japanese]. Abstracted, 1936, *Japanese Journ. Zool.*, VI, 4, p. (80).

IVES, J. E.:

1891. Crustacea from the northern coast of Yucatan, the harbor of Vera Cruz, the west coast of Florida, and the Bermuda Islands. *Proc. Acad. Nat. Sci. Philadelphia*, XLIII.

JACOBSEN, J. P. and JOHANSEN, A. C.:

1908. Remarks on the changes in specific gravity of pelagic fish eggs . . . *Medd. Komm. Havunders.*, Fisk., III, 2. København.

KARLOVAC, O.:

1936. *Parapenaeus longirostris* (H. Lucas) an der Ostküste der Adria. *Zool. Anz.*, CXV, 1/2.

KEMP, S. W.:

1915. Fauna of the Chilka Lake. Crustacea Decapoda. *Mem. Indian Mus.*, V.

LATREILLE, P. A.:

1817. Nouveau Dictionnaire d'Histoire Naturelle, XXV. *Paris.*

LINNAEUS, C.:

1767. Systema Naturae. 12th ed.

[1788. Systema Naturae. 13th ed.]

MAN, DE, J. G.:

1911. The Decapoda of the Siboga Expedition. Part I. Family Penaeidae. *Siboga-Exped.*, XIX (livr. 55 and 69).

MONTICELLI, F. S. and LOBIANCO, S.:

1900. Sullo sviluppo dei Peneidi del Golfo di Napoli. *Mon. Zool. Italiano*, XI, Suppl.

1901a. Communicazioni sui Peneidi del Golfo di Napoli. *Mon. Zool. Italiano*, XII.

1901b. Uova e larve di *Solenocera siphonocera* Phil. *Mon. Zool. Italiano*, XII.

MORTENSEN, TH.:

1897. Smaa faunistiske og biologiske Meddelelser. *Vidensk. Medd. Naturh. For. Kjobenhavn*, 1897.

NAKAZAWA, K.:

1916. On the development of *Sergestes prehensilis* Bate [Japanese]. *Dobuts Z. Tokyo*, XXVII [*vide* Gordon, 1935, p. 313].

ORTMANN, A.:

1891. Die Decapoden-Krebse des Strassburger Museums. *Zool. Jahrb.*, Abt. Syst. Geogr. Biol., V, 3.

PARR, A. E.:
1933. A geographic-ecological analysis of the seasonal changes in temperature conditions in shallow water along the Atlantic coast of the United States. *Bull. Bingham Oc. Coll.*, IV, 3.
1935. Report on hydrographic observations in the Gulf of Mexico . . . *Bull. Bingham Oc. Coll.*, V, 1.
PEARSON, J. C.:
1935. Eggs of a peneid shrimp. *Science* (n. s.), LXXXII, 2121.
PESTA, O.:
1915. Die Penaeidea des Wiener Naturhistorischen Hofmuseums. *Arch. f. Naturg.*, LXXXI, A, 1.
RAMADAN, M. M.:
1938. Crustacea: Penaeidae. *Sci. Rept. John Murray Exped.*, V, 3. *London.*
RATHBUN, M. J.:
1901. The Brachyura and Macrura of Porto Rico. *Bull. U. S. Fish Comm.* XX, (1900), part 2.
RILEY, G. A.:
1937. The significance of the Mississippi River drainage for biological conditions in the northern Gulf of Mexico. *Sears Found. Journ. Mar. Res.*, I, 1.
SAUSSURE, DE, H. L. F.:
1858. Mémoire sur divers crustacés nouveaux du Mexique et des Antilles. *Mémoire pour servir a l'histoire naturelle du Mexique*, etc., I, 1. *Geneve et Bâle.*
SAY, T.:
1817. An account of the Crustacea of the United States. *Journ. Acad. Nat. Sci., Philadelphia*, I, 1.
SCHMITT, W. L.:
1935. Crustacea Macrura and Anomura of Porto Rico and the Virgin Islands. *Sci. Surv. Pto. Rico. & Virgin Ids., New York Acad. Sci.*, XV, 2.
SCHOTT, G.:
1926. Geographie des Atlantischen Ozeans. *Hamburg.*
1935. Geographie des Indischen und Stillen Ozeans. *Hamburg.*
SEBA, A.:
1758. Locupletissimi Rerum Naturalium Thesauri . . III. *Amstelaedami.*
SMITH, S. I.:
1886. On some genera and species of Penaeidae, mostly from recent dredgings of the United States Fish Commission. *Proc. U. S. Nat. Mus.*, VIII (1885).
SOESIMA, I.:
1926. Embryology and ecology of *Acetes japonicus* of Ariake Bay. [Japanese]. Abstracted, 1928, *Japanese Journ. Zool.*, I, 6, p. (173).
STEBBING, T. R. R.:
1893. A History of Crustacea. Recent Malacostraca. *Internat. Sci. Series*, LXXI. *New York.*
STEPHENSEN, K.:
1923. Decapoda-Macrura excl. Sergestidae. *Rept. Danish Oc. Exped. 1908–10*, II, D. 3.

SUND, O.:
1920. Peneides and Stenopides. *Rept. Sci. Res. "Michael Sars" North Atlantic Deep Sea Exped.*, III, 2.

THALLWITZ, J.:
1891. Decapoden-Studien. *Abhandl. u. Berichte des kön. Zool. und Anthropol.-Ethnogr. Museums zu Dresden* 1890/91, No. 3.

VERRILL, A. E.:
1922. Decapod Crustacea of Bermuda. II. Macrura. *Trans. Connecticut Acad. Arts & Sci.*, XXVI.

VIOSCA, P. P.:
1920. Report of the biologist. *Bienn. Rept. Dept. Cons. Louisiana*, IV.

WEYMOUTH, F. W., LINDNER, M. J. and ANDERSON, W. W.:
1933. Preliminary report on the life history of the common shrimp *Penaeus setiferus* (Linn.). *Bull. U. S. Bur. Fish.*, XLVIII, 14.

WHEELER, J. F. G.:
1937. Further observations on Lunar Periodicity. *Journ. Linn. Soc. London*, Zool., XL, 272.

Contribution No. 204

BULLETIN OF THE GEOLOGICAL SOCIETY OF AMERICA
VOL. 50, PP. 1395-1422, 3 PLS., 4 FIGS. SEPTEMBER 1, 1939

FORAMINIFERA OF SUBMARINE CORES FROM THE CONTINENTAL SLOPE

BY FRED B PHLEGER, JR.

CONTENTS

Page
Abstract ... 1396
Introduction ... 1396
  General statement ... 1396
  Acknowledgments ... 1397
Locations of cores ... 1397
Method of study ... 1398
The foraminiferal fauna ... 1400
  General statement ... 1400
  The Recent foraminiferal fauna ... 1400
  The Arctic foraminiferal fauna ... 1402
  Discussion of species ... 1402
Faunal data ... 1406
  General statement ... 1406
  Line south of Cape Cod ... 1406
  Delaware Bay group ... 1407
  Chesapeake Bay group ... 1411
Interpretation of faunal data ... 1411
  General statement ... 1411
  The Arctic fauna ... 1413
  Postglacial warm-water fauna ... 1415
  Pelagic and benthonic types ... 1416
Conclusions ... 1418
Works to which reference is made ... 1418

ILLUSTRATIONS

Figure
1. Map showing locations of submarine cores ... 1398
2. Relative water temperature indicated by faunas in northerly line of cores ... 1408
3. Relative water temperature indicated by faunas in Delaware Bay group of cores ... 1410
4. Relative water temperature indicated by faunas in Chesapeake Bay group of cores ... 1412

Plate — Facing page
1. Species typical of warm-water samples ... 1420
2. Species typical of Arctic samples ... 1421
3. Species occurring commonly in both warm-water and Arctic faunas ... 1422

ABSTRACT

The foraminiferal fauna in more than 35 submarine cores, collected by H. C. Stetson from the continental slope of the western North Atlantic, have been examined to determine the areal and vertical extent of present and previous assemblages. Below the present fauna, recorded at the top of the cores, there is a widely distributed fauna of Arctic to sub-Arctic aspect not now living in this area. This fauna is similar to the one reported from the Georges Bank canyons and from a core in this area, and is identified by Cushman as Pleistocene. This Pleistocene fauna is probably of Wisconsin age, since it lies directly beneath the present fauna. At the western edge of the basin of the North Atlantic ocean, beyond the continental slope, two Arctic faunas have been recognized below the Recent assemblage and are separated by a pelagic warm-water fauna typical of the present Gulf Stream region. This may represent two Pleistocene stages or it may indicate separate maxima of the last stage.

In a few cores a foraminiferal fauna is recorded a short distance beneath the surface in which pelagic types characteristic of warm surface water are considerably more abundant than in the present-day assemblage. This suggests a possibility of a postglacial shift in warm surface water areas.

New information concerning distribution suggests that water temperature may be the most important regulating factor in the occurrence of many Foraminifera.

INTRODUCTION

GENERAL STATEMENT

Recently, while examining various submarine cores for Foraminifera, Cushman observed an Arctic foraminiferal fauna at a short distance from the top of some of the cores taken from the Georges Bank canyons, in a core about 100 miles southeast of New York City, and in the cores collected by Piggot across the North Atlantic at the position of the cable crossing. In all these occurrences the implication has been that the Arctic fauna (or faunas) represents accumulation during the Pleistocene glaciation.

It has seemed desirable to check these discoveries with further submarine exploration. Accordingly the writer was given the opportunity of studying the Foraminifera of several cores collected by H. C. Stetson of the Woods Hole Oceanographic Institution during 1938 and subsequent seasons. All the present cores, taken with the coring gun developed by Piggot, attain a maximum length of 10 feet (3 meters); the average length is about 7 feet (2 meters).

The main purpose of this study has been to ascertain whether an Arctic foraminiferal fauna or faunas occurs in cores taken some distance south of most previous ones, and, if so, the areal distribution. A study of the sediments is being undertaken by Stetson. The present paper is concerned only with the Foraminifera in the cores and their direct bearing on Recent and past conditions in this area of the Atlantic. A study of this type should have an important bearing upon the interpretation of marine conditions during the time that such an Arctic fauna was deposited. For the present report all but one core are from a section of the continental slope of the western North Atlantic. The collected material is still considered incomplete, even for the continental slope. Inasmuch as this and related researches will continue for some time, it is considered timely to present a summary of the present contributions. Before any far-reaching conclusions can be established it will be necessary to continue the coring and faunal study of the continental slope and the ocean basin.

ACKNOWLEDGMENTS

A considerable part of this work was done at the Woods Hole Oceanographic Institution during the summer of 1937, and the writer is grateful to that institution for facilities and other aid in research. The writer is particularly grateful to Henry C. Stetson who has generously placed the core faunal material at his disposal and has been most helpful in other ways; and to Dr. Joseph A. Cushman for the use of his laboratory and equipment and for many useful suggestions. Many of the faunal data have been discussed at length with Miss Frances Parker, who is conducting a closely allied research. The generosity of the Geological Society of America in awarding a grant from the Penrose Bequest has made continuation of this work possible.

LOCATIONS OF CORES

All the cores here discussed came from the continental slope, from a position east of New Jersey to east of Chesapeake Bay (Fig. 1). They are in three groups: The 1936 cores run in a line south of Cape Cod, beginning at about 40° N. Lat. or about 100 miles due south of Martha's Vineyard. Thirteen cores were collected from this traverse, but only 10 are here discussed. One group of the 1938 cores, 11 in number, is more or less parallel to the coast line at a position east and slightly north of Delaware Bay. The third group, consisting of 9 cores, is east and slightly north of Chesapeake Bay. The geographic position of each core, as recorded in the deck log of the "Atlantis," is given in Table 1.

The depth of the cores ranges from slightly beyond the break in slope at 215 meters to the eastern part of the ocean basin at 3900 meters. This is a complete traverse of the continental slope, and this range in depth is shown only in the more northerly line. The southerly group ranges in depth from 402 to 1990 meters and represents primarily the upper two-thirds of the slope.

An attempt was made in 1938 to collect in view of the rugged submarine topography shown on recent maps compiled by Veatch and Smith (1939). This was done largely to examine the comparative rates of deposition, if possible, in the valleys and on the divides of the canyons there present. At Veatch's suggestion a series of traverses were made across certain of the valleys which he had contoured. As a result the cores are placed parallel to the coast line and are quite variable in depth. In some cases it was difficult to locate exact positions in relation to the submarine topography due to the difficulty of obtaining an exact position at sea by ordinary methods. This probably accounts for the variations in depth observed between the depths here given and those shown by the topography if the positions are plotted on Veatch's maps.

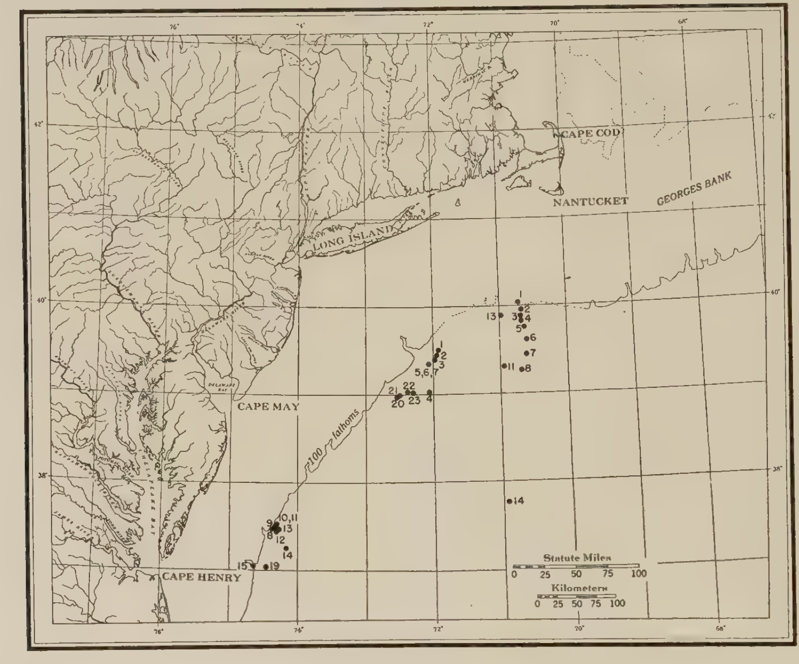

76°
74°
72°
70°
68°
42°
40°
38°
CAPE COD
NANTUCKET
GEORGES BANK
LONG ISLAND
DELAWARE BAY
CAPE MAY
100 fathoms
CHESAPEAKE BAY
CAPE HENRY
1
2
3
4
5
6
7
8
11
13
14
5,6,7
21
22
20
23
9
10,11
12
15
19
Statute Miles
0 25 50 75 100
Kilometers
0 25 50 75 100

FIGURE 1.—*Map showing locations of submarine cores*

The smaller numbers are the 1938 cores. (Base map by courtesy of the United States Coast and Geodetic Survey.)

METHOD OF STUDY

Cushman, Henbest, and Lohman (1937) have commented upon the possibilities of the mixing of the sediments, and consequently the microfaunas, in the coring of the bottom. It is obviously of importance to know whether true vertical relationships between samples are shown. They have concluded that the only zone of mixing occurs around the outer surface of the cores because none or only a few of the species present in the bottom sample of their core occur at the top.

In the present writer's experience the above conclusions are correct and are supported by the following observations: (1) In cores in which there is a succession of layers of sediments of different colors or texture, a thin film of the lower layers coats the outside of the core at the position of the upper layers. This is particularly noticeable in core 21-38 in which white Eocene material underlies a gray mud; a thin layer of the white sediment coats the darker material above for a few inches vertically. The thickness of this outside veneer is about one-sixteenth of an inch. (2) There is no disturbance of thin layers where they can be observed. In some cases there is a slight drag on the outside of the cores, but this is confined to the outer fraction of an inch.

Table 1.—*Locations and depths of cores*

Core	N. Lat.	W. Long.	Depth	Length of core
1	40° 1′	70° 42′	215 meters	85 cms.
2	39° 57′	70° 41′	395 meters	289 cms.
3	39° 53′	70° 41′	647 meters	289 cms.
4	39° 50′	70° 41′	1050 meters	244 cms.
5	39° 45′	70° 39′	1954 meters	91 cms.
6	39° 36′	70° 36′	2250 meters	106 cms.
7	39° 26′	70° 37′	2579 meters	225 cms.
8	39° 15′	70° 42′	2740 meters	109 cms.
11	39° 18′	70° 57′	2660 meters	194 cms.
13	39° 53′	70° 58′	556 meters	190 cms.
14	37° 42′	70° 53′	3900 meters	299 cms.
1–38	39° 30′	71° 53′	1097 meters	244 cms.
2–38	39° 27′	71° 56′	1325 meters	132 cms.
3–38	39° 24′	71° 57′	1025 meters	264 cms.
4–38	39° 02′	72° 01.5′	1042 meters	115 cms.
5–38	39° 21.5′	72° 02′	1160 meters	149 cms.
6–38	39° 20.5′	72° 03.5′	1710 meters	175 cms.
7–38	39° 19′	72° 05′	1125 meters	156 cms.
8–38	39° 28.5′	74° 23′	660 meters	110 cms.
9–38	37° 27′	74° 24′	542 meters	143 cms.
10–38	37° 25′	74° 27′	878 meters	187 cms.
11–38	37° 24′	74° 28′	402 meters	138 cms.
12–38	37° 21′	74° 21′	1450 meters	147 cms.
13–38	37° 22′	74° 20′	1080 meters	124 cms.
14–38	37° 17′	74° 09′	1990 meters	148 cms.
15–38	37° 03.5′	74° 38′	610 meters	183 cms.
19–38	37° 02.2′	74° 29′	1430 meters	175 cms.
20–38	38° 57.5′	72° 30′	1455 meters	208 cms.
21–38	38° 58′	72° 28.5′	1565 meters	157 cms.
22–38	39° 02′	72° 21.5′	860 meters	171 cms.
23–38	39° 01.5′	72° 17′	1665 meters	235 cms.

In sampling, every reasonable precaution has been taken to prevent contamination within and between cores. As the cores come out of the gun they are sealed in a brass tube the diameter and length of the core itself (Piggot, 1936). This is carefully split with several sheets of iron which have been sharpened on one edge, and two equal halves are obtained. After one of these cutting tools has been used it is thoroughly washed to remove any mud or sand. The only mixing which might occur is a horizontal one, and some of the veneer of material coating the outside may be spread on the flat surface of each half.

In taking samples for study of the Foraminifera only a quarter section of a core has been used, and of this a piece has been taken up to a maximum length of 10 cms. One-eighth to three-sixteenths of an inch has been carefully removed with a knife from all the outer surfaces of each sample. With these precautions the sample obtained is considered accurate. The vertical positions of the samples within the cores have been determined, where possible, on variations of lithology. In those cores which exhibit no apparent change in lithology the samples were taken at top, middle, and bottom.

THE FORAMINIFERAL FAUNA

GENERAL STATEMENT

It is not the purpose of this paper to deal in detail with the areal distribution of the foraminiferal fauna of the continental slope. Considerable work of this kind has been done by Cushman (1918-1931) and is being continued by Cushman and by Miss Frances Parker at the Woods Hole Oceanographic institution. In the accompanying faunal charts (Tables 2, 3) are listed species which occur in most or a large number of the core samples. This list represents less than one-third of the total number of species observed in the entire suite of samples. All those omitted are so relatively rare that it has not been considered necessary to include them in this paper. From plotting of the data of their occurrence it cannot be shown at the present time that they have any significance in the problems at hand. No attempt is made, moreover, to describe in detail the various species listed. In some cases brief distinguishing features are mentioned in the important forms, and remarks on distribution are included which seem pertinent to the problems. Only those species are figured which are either diagnostic in this type of study or are so prevalent over a large area that they cannot be ignored. All identifications have been verified at the Cushman Laboratory for Foraminiferal Research.

THE RECENT FORAMINIFERAL FAUNA

The Recent foraminiferal fauna occurs in the bottom sediments deposited since the Pleistocene and is present in the top of all the cores, extending downward for a varying distance. The average sample from the continental slope sediments is characterized by an abundance of individuals of typically pelagic forms, particularly of the families Globigerinidae and Globorotaliidae. Other types occur in abundance but are not so widespread as these; the Orbulininae are widespread and fairly abundant but rarely constitute a very large percentage of any sample.

TABLE 2.—*Distribution of Foraminifera in northerly line of cores*

CORE	1		2				3					4				5		6			7						8				11							13				14							
Sample	1	2	1	2	3	6	1	2	3	4	9	1	2	3	7	1	2	1	2	4	1	2	3	5	7	10	1	2	3	6	1	3	4	5	6	7	8	1	2	3	7	1	3	4	5	8	11	15	21
Saccammina sphaerica			R	R			R					C									R																	R											
Proteonina difflugiformis							R					C																										R				C							
Eggerella																																R	R	R		R						R							
Textularia												R																			R			R															
Listerella occidentalis	C			C														R				C	R				A	R			C	C			R							C							
L. communis	R		A				R																															A	A										
Karreriella bradyi							R	R				C	C														C	C	R									R											
Quinqueloculina seminulum								R	R	A	R		R																			C	R																
Q. sp.		C																															R	C	R							R							
Triloculina tricarinata					R								R	R				R										R															R						
Pyrgo subsphaerica					C	R		R	R	R	R		R	R		R		R				C					R	R	R	C	R	R	R	C	R		A			C									
Other pyrgos				R																		A	R	R			R	R															R						
Robulus	C	C	R												R	R	R																	R				R	R										
Marginulina bachei	C	R	R																																														
Lagena			R	R	R	R		C	R	R		R	R	R								R					R		R						R	R	R	R	R										
Nonion cf. grateloupi			R		A	C	R	A	A	C	C	C	R	R	C		R																							R	C								R
N. labradoricum			C		C	C	R	A	R	A	C	R	A	A	C		C			R	C			A	A			C	A			R		R	R	R		C	A	A	C						R		
N. pompiloides	R	C		R																								R				A																	
Elphidium sp.			C				R	R		C	R	R	R		R		A	R		A	R		A	A	A	A		A	C	A		A		A	R	C				R	R						R		
E. advenum var. *margaritaceum*		A	R	R	A	A	R	A	A	A	R		A	A	R	R	R	C	A	A	C		A	A	A	C		A	A	A						C			R	C	A								
Bulimina marginata	A	A				R			C					R	R																																		
B. aculeata			A	R	R		A	A	R			A	A			C	C				R			C	C			R	C				A	A	R	A	C	C	C	A									
B. cf. affinis	A		C	A			R	A	R	R	R		A	C	C		C	R	R	R	A	A		A	R		A	A	A		A	A	A	A	A	C	C	A	A	A	R			R					
B. inflata				R	R												R				R			C					C			R	R	C	A	R	R												
Uvigerina		R	C		C		A	C				A	A	R	R	R	R	A	R		A	C	C	A		R	C	R	C		A	A	A	A	A	A	A	C	C	R									
Angulogerina angulosa	A	A	R			R										R	A												C																				
A. sp. 1							A	R	R			R																											R										
Buliminella elegans var. *exilis*			A	A	A	A	C	R	C	C	R	R	C	A	C	C	R	R	R	R	R	R		C	A	R			R	R		C	A	A		R		C	R	A	A			C					
Virgulina schreibersiana	A																																																
V. squammosa			R	R			R	C	C	R			R	R																R										R	R			A			R		A
Bolivina subaenariensis	C	R					R		R					C																			C																
B. subspiniscens												R																																					
B. sp. 1	A							R	R	R		R	R																R										R		R								
Gyroidina soldanii	A			R			C	R				C	C	R	R			R	R								R		R									A	A	R									
Rotalia cf. beccari																																																	
Eponides				A								R		R		R		R	R		C	R	R				A	R	R		C			R								C							
Cassidulina laevigata		A	C		A	A	R	A	A	A	A		A	A	A	R	A		C	A	R			A	A	A		R	A	A			A	C	A	A	A		A	A	A							R	
C. subglobosa		A	R		C	A		C	R	A	A			A	C					R																				R									
Cassidulinoides bradyi	C																																																
Globigerina bulloides	A	C	A	A	C	A	A	A	A	C	C	A	A	A	C	C	C	A	A	C	C	A	A	A	A	R	A	A	C	R	A	A	A	A	A	A	A	C	A	C	R	A	A	A	A	C	A	C	A
G. inflata	A	C	A	A	C	R	A	A	A	R	R	A	A	A	R	C	A	A	A	R	A	A	A	A	R	R	A	A	A	C	A	A	A	A	A	C	R	A	A	A	A	A	C	A	R	C	A	R	A
G. dubia	A	R		C	R		A	A			R	A	C		R	C	R	A	A	R		A	A				C	A	A	R	A	A	A	A	A	A	R	C	A					A	R	R	R	R	A
G. pachyderma			R		A	A		C	A	A	A		A	A	A		A	C	C	A			R	A	C	A		A	A	A		C	C	R	R	C	C	C	R	A	A		C		A	A	C	A	A
Globigerinoides rubra			R	A				R	R			R	R					C	R		R	R	C	R			A	A	R		C	C	R		R				R			A		C	R				C
G. conglobata	C		A	A			C	C	R			C				C		A	C			A					A	C	A			C	R					C	C			A		C					
G. sacculifera		R	R													C		C									C	R	R					R						R		C		A	R		C	C	
Globigerinella aequilateris								R								R																	R									R		A					
Orbulina universa	C		A	A			R	R	R			C	R			C	R	A				A	C	R	R		C	C	C		C	C	C	C	C	C	R	R	C	R		A		A					
Globorotalia menardii	A		A	A			C	C	R			A				A		A	C		A	A	C				A	R	A		A	R		C	A	R		A	A			A		A					
G. truncatulinoides			C	A			C	R				C	R			C	R	C	R		R	A	R	C			A	R	A			R	R	A	R	A		C	R					C					
G. tumida			R				R					C				A		R									C		C									C				C		R					
G. hirsuta				R			C	R				C						R	R				R	R								R		C		R		R							R				
Pullenia quinqueloba			C				R					C	R			R	R										A	R				R				R		C											
Pulleniatina obliquiloculata			R	R				R				C				R		R	R			C	R				R		R		R			R					R					R					
Sphaeroidina bulloides							C	R				R	R																R										A	R									
Cibicides pseudoungeriana	A		R				R	C				A				R		C	R								C											C	A	R									
C. lobatulus		A																											A																				

A=abundant; C=common; R=rare.

species cannot be used in distinguishing warm and cold water in the cores, however, since in many cases they occur in similar abundance in radically different faunal assemblages. Also their distribution in present waters is not so restricted as the species already listed. Other species also occur in abundance in some of the samples, but their presence is areally restricted, and most also occur in colder water assemblages.

Another characteristic feature of the Recent samples is the generally large number of species. It is not uncommon to have 60 species or more in one small sample. Particularly observable are the arenaceous forms. The warm-water specimens are occasionally large, especially in the Globorotaliidae, and also in *Nodosaria* and *Listerella*. These latter characteristics are in some cases quite useful supplementary criteria in the determination.

THE ARCTIC FORAMINIFERAL FAUNA

Beneath the top of most of the cores a fauna radically different from the Recent is present, at approximately 40 cms. beneath the top in some and not above 150 cms. in others; in a few cases it is not present although a 200 cm. section has been obtained. This fauna is composed of species living at the present time, but some are not present in the Recent fauna in the area covered by the cores. This lower fauna is at present essentially restricted to regions of cold water, mostly within the Arctic Circle or adjacent regions (Cushman, *et al.*, 1937). The most obvious general aspects of the fauna in comparison to the Recent are the relatively fewer Globigerinidae, the near or complete absence of the Globorotaliidae, and *Orbulina*, the smaller complete population, and the fewer species present. The following species, occurring commonly or in abundance, are characteristic:

Globigerina pachyderma
Elphidium advenum var. *margaritaceum*
E. sp.
Cassidulina laevigata
Cassidulina subglobosa
Nonion labradoricum
Virgulina squammosa
Bolivina sp. 1

The last three species are somewhat restricted in their usefulness and must be used with care. As this work has proceeded it has become increasingly apparent that it is difficult to apply any very strict rules in distinguishing these faunas. In every case the cold-water nature of the lower fauna, where present, has been determined relative to the Recent in the same core. In general the above criteria hold very well, but each core presents a more or less distinct problem in this connection.

DISCUSSION OF SPECIES

The more important species are illustrated in Plates 1, 2, and 3. Notes on some of these follow:

Pyrgo subsphaerica d'Orbigny

(Plate 3, figure 20)

Comparatively rare form, mostly present in cooler water samples.

Nonion cf. *grateloupi* (d'Orbigny)

(Plate 3, figures 7, 8)

Rather widely distributed in the Recent samples and also in the sections considered Arctic. Previous data show a more limited distribution.

Nonion labradoricum (Dawson)

(Plate 2, figures 13, 14)

Generally characteristic of the Arctic assemblages but also occurs in the Recent samples. Present data indicate that it is probably more common this far south than previously recorded.

Nonion pompiloides (Fichtel and Moll)

(Plate 3, figures 3, 4)

Relatively rare and in most cases does not occur in the fauna at the top of the cores.

Elphidium sp.

(Plate 2, figure 11)

Includes forms with a heavier and more opaque test than in *Elphidium advenum margaritaceum,* and probably more than one species. Wide areal and depth distribution in the present cores; particularly characteristic of the Arctic assemblages but also rare in a few Recent sections down to 2500 meters.

Elphidium advenum var. *margaritaceum* (Cushman)

(Plate 2, figure 12)

Forms included under this name are characterized by a more delicate, thin-shelled, and punctate test than the forms included under *Elphidium* sp. Possibly more than one species is here included, but further subdivision has not appeared necessary at present. Abundant in the Arctic fauna and also in transition phases between cold and warm-water assemblages. Very wide depth and areal distribution in the lower sections of the present cores. Common in the top of core 7, which was collected in water having a depth of 2579 meters, and recorded at the top of core 6-38, at 1710 meters.

Bulimina marginata (d'Orbigny)

(Plate 3, figure 23)

Common in some Recent samples, mostly in moderately shallow water, and occurring in a few Arctic samples.

Bulimina aculeata (d'Orbigny)

(Plate 3, figure 24)

Wide depth and areal distribution in Recent and older cold-water samples.

Bulimina affinis d'Orbigny

1922. *Bulimina affinis* Cushman, U. S. Nat. Mus., Bull. 104, p. 103, pl. 20, fig. 6.

Very wide distribution in Recent and older core samples. More than one species probably here included.

Uvigerina peregrina Cushman

(Plate 3, figures 5, 6)

Abundant in more southerly cores, with greater abundance in Recent samples. Very variable in degree of ornamentation, from costate to almost entirely spinose.

Angulogerina angulosa (Williamson)

(Plate 3, figures 10, 11)

Particularly common in Recent samples of cores from comparatively shallow water but also observed in a few cases in Arctic assemblages from deeper water.

Angulogerina sp. 1

(Plate 3, figures 12, 13, 14)

A smaller, more slender, and more costate species than *Angulogerina angulosa;* recorded abundantly in the Recent samples down to 1450 meters.

Cassidulina laevigata d'Orbigny

(Plate 2, figures 6, 7, 8)

Rare to common in Recent samples but constituting a large percentage of the cold-water samples in the cores. Wide distribution at present, but from published records appears to be most prevalent in cooler waters (Cushman, 1922, p. 122) and is common in the Arctic. Has a greater depth range in the present Arctic assemblages than *Cassidulina subglobosa.*

Cassidulina subglobosa H. B. Brady

(Plate 2, figures 3, 4)

Common or abundant in many of the Recent shallower water core samples and more abundant in the Arctic assemblages, particularly in cores taken from moderate depths. Apparently more or less characteristic of the upper part of the continental slope.

Globigerina bulloides d'Orbigny

(Plate 3, figures 15, 16)

Most consistently abundant single species, occurring in all the samples and therefore of no significance in temperature determinations.

There has been considerable confusion as to what should be referred to this name; the present species is not true *Globigerina bulloides* but is the form which goes under that name in this part of the Atlantic. The writer's identification is based largely upon Cushman (1924, Pl. 2, fig. 1-4). If several species are represented in the present samples they are so nearly alike that they would be of doubtful use in the present study.

Globigerina inflata d'Orbigny

(Plate 3, figures 18, 19)

Also very abundant in most of the samples. Cushman (1924, p. 13) assumes it to be a benthonic form since it does not live in the tropics and therefore does not have the same distribution as species of *Globigerinoides.* Common in the present cold-water assemblages but a little less so in the Recent samples in most cases.

Globigerina dubia Egger

(Plate 1, figures 14, 15)

Abundant in samples which contain a warm-water assemblage but also occurs in other samples. Most common along the path of the Gulf Stream and less so on the continental slope.

Globigerina pachyderma Ehrenberg

(Plate 2, figures 1, 2)

Recorded from the Arctic by Brady and from the Antarctic by Pearcey, its distribution is thought to be entirely confined to cold waters. Brady did not find it in the pelagic tows in the Arctic but only in the bottom samples and on that basis it is considered to be of benthonic habitat (Cushman, 1924, p. 15).

Characterized by the four outside chambers with slightly depressed sutures, with the aperture slit-like along the last formed chamber; the surface of the test has a granular appearance, and the wall is quite thick. Considered one of the most useful forms in identifying cold-water assemblages in the cores.

Globigerinoides rubra d'Orbigny

(Plate 1, figure 12)

A common tropical water and Gulf Stream form found in some abundance on the continental slope. The test in many cases is not so pink as in warmer waters and it is likely to be confused with *Globigerinoides sacculifera.* May be distinguished from the latter species, however, by the difference in surface ornamentation of the test. A good indicator of warm surface water and does not occur in typically cold-water samples from the present cores.

Globigerinoides sacculifera H. B. Brady

(Plate 1, figures 16, 17)

Common in the Recent core samples, particularly near the Gulf Stream region. Not present in the Arctic assemblages and therefore a good indicator of warm surface water. Distinguished by the projected last chamber, and in specimens lacking this by the reticulate character of the surface of the test. Typical of very warm-water areas at the present time.

Globorotalia

Globorotalia is quite abundant in the Recent samples underlying surface areas of warm-water, and the species are among the most useful indicators of such in the present cores. The species are sufficiently distinctive to separate easily (Pl. 1, figs. 3-7, 10, 11). In general, the specimens are large.

Buliminella elegans var. *exilis* (H. B. Brady)

(Plate 3, figure 17)

Abundant to rare in most samples, except in the deepest cores studied.

Virgulina squammosa d'Orbigny

(Plate 2, figure 10)

Most common in more southerly core groups. Greatest abundance characteristic of cold-water fauna in many cases.

Cibicides pseudoungeriana (Cushman)

(Plate 3, figures 1, 2)

Typical in warm-water assemblages. Very abundant in many Recent samples.

Globigerinella aequilateris (H. B. Brady)

(Plate 1, figures 11, 13)

Rare in the present cores, but where present probably quite indicative of warm surface water conditions, judging from the known distribution of the species.

Pullenia quinqueloba (Reuss)

1924. *Pullenia quinqueloba* Cushman, U. S. Nat. Mus., Bull. 104, pt. 5, p. 42-43, pl. 8, figs. 5-9, 11.

The distribution given by Cushman (1924, p. 43) "seems to be in cold deep waters as a rule." Occurs in the Recent fauna over most of the depth range covered by the cores and is in most cases absent from the Arctic assemblages.

A variety of arenaceous forms occur mainly in the warm-water samples, only a small number of which are listed in Tables 2 and 3. These constitute a very minor percentage of the census and have not been used to any extent in the present study.

FAUNAL DATA

GENERAL STATEMENT

This part of the work on the present cores is concerned entirely with the foraminiferal microfaunas and their direct implications. The detailed sedimentary data enter into the general conclusions and are to be presented elsewhere. The following deals with a discussion of the faunas by cores. The data are presented graphically in Tables 1 and 2 and in Figures 2, 3, and 4.

LINE SOUTH OF CAPE COD

Core 1. The top sample has a warm-water fauna somewhat different from that farther down on the slope. Few Globorotaliidae are present, and there is an abundance of *Bulimina,* together with *Angulogerina* and *Bolivina* sp. 1. The sample at the bottom, 80-85 cms., carries a fauna considered of probable Arctic type, although the typical *Globigerina pachyderma* was not observed; *Elphidium advenum margaritaceum* and *Cassidulina* are abundant, and warm-water species are rare. It probably represents a transition fauna.

Core 2. The top sample has a moderately warm assemblage, but at 30-40 cms. is a fauna which appears to be of warmer type, since *Elphidium* and *Cassidulina* are present in the top and absent in this lower section. At 63-70 cms. is a definitely Arctic assemblage continuous in all sections to 289 cms.

Core 3. The trend toward cold-water types is evident at 30-34 cms. (sample 2) in the introduction of *Globigerina pachyderma* and the abundance of *Elphidium* and *Cassidulina.* At 63-70 cms. the fauna is definitely Arctic, but *Globigerinoides rubra, G. sacculifera,* and *Orbulina universa* are present. This sample is considered a true transition between the two types, above and below. From here the Arctic assemblage is present to 289 cms. Core 13 shows about the same vertical distribution, but an unusual abundance of *Globigerina pachyderma* at the bottom (180-190 cms.) may suggest very cold water. In core 4 the Arctic fauna is met at 35-42 cms., and cold-water species increase in abundance toward the bottom of the core (244 cms.).

A	C	C	C	R					C	R	C	R		R	C	C
	R	C	R			A	R	C	R	R	C	R	R			
A	A		A						R		A		A		R	
											R	R				
				R			A	C		R	R	R			R	
	A		C										C		R	
C	C		A	A	R	R	R	C	A	A	A	A	C	A	A	A
			R			C	R	R								
	A	A	C	A		R			A	A	A	A	R	C	R	A
R	R	R	C	C	R	A	A	A	R	R	R	C		R	R	R
A				R		C			R					A	R	R
R		R		C					R		C	R	R	A	C	C
A				R			C					A				
R	R	A	R	R		A	A	C	R	R	R	C		R	R	
	A			R		A	A	A		R	R	A	R	R		
						R			R							
A	A	A	A	A		A	A	A	A	A	A	A	A	A	A	A
A	A	A	A	A		A	A	C	A	C	A	C	A	A	A	A
R			R	C	A	R	C		C			R	C	C	R	
		A		C						R		R			C	C
R	C	R	R	R	A	C	R	A	R		R	R		R	C	
R	C		R	C	A	R		R					R	R	R	
					R			R								
C	C			C	A	R		A	R	R	R	R	R		R	
C	A		C	A		R	R			R	R		C	R	R	R
R			R				R	R	R	R			R			
						C								R		
C			R								R					
R																
			R	R		R										
															R	
R	A		R	R		R	A	A	R		A	C	R	R	R	R
								A								

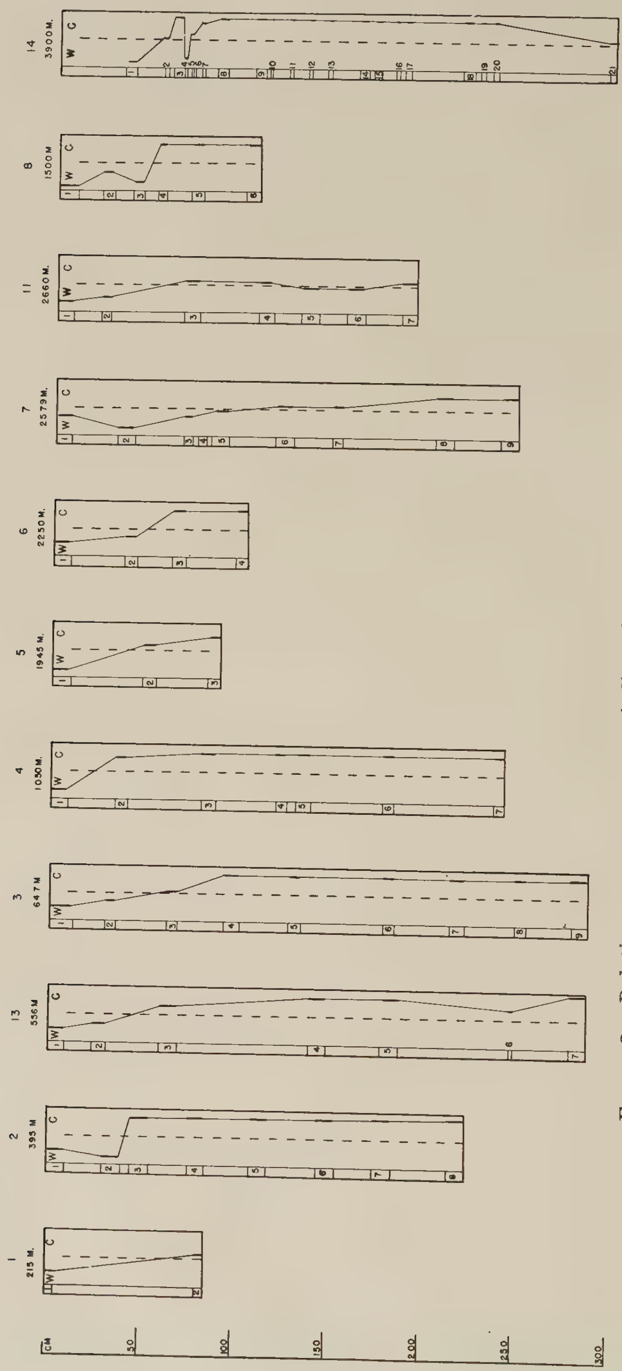


FIGURE 2.—*Relative water temperature indicated by faunas in northerly line of cores*

W = warm water; C = cold water.

water fauna. Core 3-38 has a slightly warmer water fauna at the top, and an Arctic fauna appears at 111-119 cms., continuing to 264 cms. At the bottom the fauna is interpreted as indicative of colder-water conditions than that shown in core 1-38 or in the upper part of the same core. This latter conclusion is based upon the concentration of typically cold-water types to the exclusion of any other species.

Core 2-38. The faunal evidence is confusing, but the writer's tentative interpretation is that the fauna of the entire core borders on an Arctic type. If this is true, the Recent fauna is not represented at all. Core 4-38 shows much the same condition, but in the top section Arctic and warm-water types are definitely mixed. This condition also holds for the bottom section at 107-115 cms. but is not true for the middle section at 55-63 cms.

Core 5-38. This has a greater variety of warm-water forms at 61-70 cms. than at the top and is interpreted as indicative of warmer-water conditions than the Recent assemblage. A typically Arctic fauna occurs from 98-117 cms. and 119-126 cms. A trend toward a warmer fauna is seen in the introduction of *Globigerinoides rubra* and *Orbulina universa,* while at the bottom (144-149 cms.) a definite warm-water fauna is present.

Cores 6-38 and 7-38. They likewise have a greater number of warm-water species below the top than in the top sections, at 111-118 cms. and 81-88 cms. respectively. In the former core, which is also the longer one, there is a rather abrupt transition to an Arctic assemblage at 122-130 cms., and this continues to the bottom, at 175 cms. The lower sections of this core are notable for the few species and the relatively few individuals. Core 7-38 shows a trend toward an Arctic fauna at the bottom (146-156 cms.) but this is concluded mainly on the basis of the paucity of species and individuals.

Core 20-38. The cold-water types appear at 92-100 cms. and continue to the bottom (208 cms.), with a colder assemblage in the two lower sections than in the two directly above.

Core 22-38. The section at 68-76 cms. is suggestive of warmer conditions than that at the top. At 105-112 cms. a transitional fauna is present, and an Arctic fauna occurs from 127-171 cms. In core 23-38 the Recent fauna is uniform in the upper 131 cms., and a uniformly Arctic fauna is present in the bottom part (148-235 cms.).

Core 21-38. This contains a Recent fauna in the upper 114 cms. The lower part (123-157 cms.), however, contains a fauna which has *Hantkenina* and is distinctly Tertiary in aspect, probably Eocene. A few species were observed by the writer which appear close to Cretaceous forms. The fauna is somewhat unique and is being described by Cushman. The Eocene fauna occurs in a white rather hard matrix. At 120-

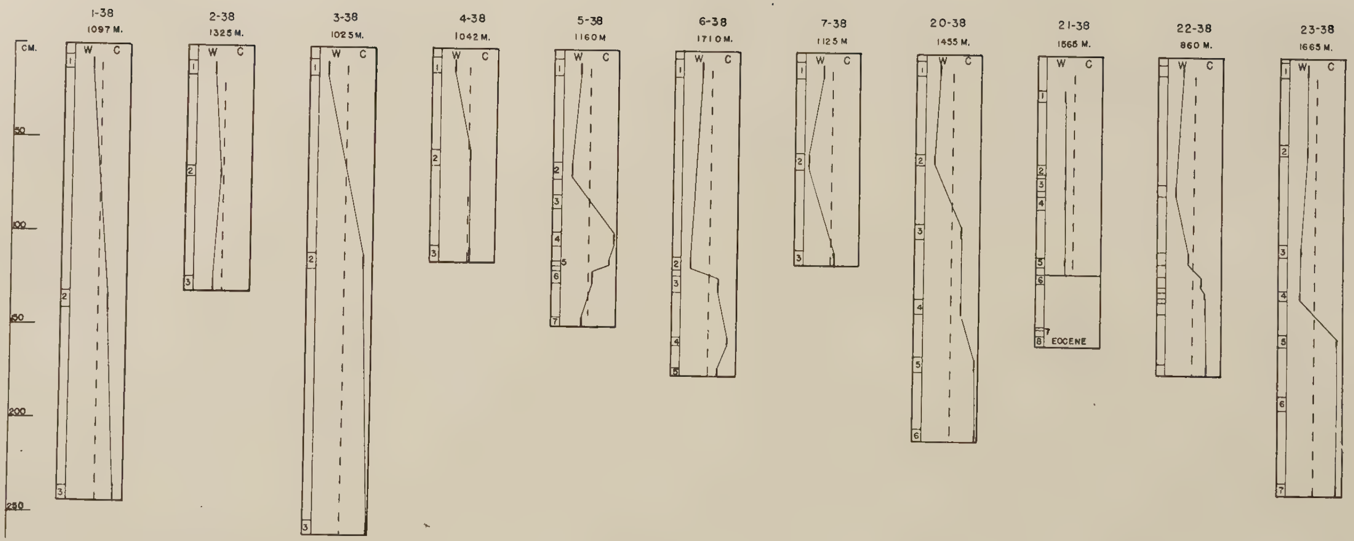


FIGURE 3.—*Relative water temperature indicated by faunas in Delaware Bay group of cores*

W = warm water; C = cold water.

121 cms. a band of this white material is separated from the bottom section by 2 cms. of the dark fine-grained sediment containing the Recent sediment in the upper part of the core. In this white band occurs a mixture of the Eocene and Recent species.

CHESAPEAKE BAY GROUP

Cores 8-38, 9-38, 10-38, and 11-38. They have lengths of 110 cms., 143 cms., 187 cms., and 138 cms. respectively and did not penetrate the Recent fauna. The warm-water assemblage throughout is typical of the continental slope. In core 11-38 the fauna in the lower section, from 66-134 cms., is thought to represent a slightly warmer assemblage since *Globigerina dubia* is abundant in this range and was not observed in the top section.

Core 12-38. This has a distinctly warmer assemblage at 100-108 cms. than at the top and contains a cold-water fauna at 139-147 cms. In core 13-38 the Arctic assemblage appears at 66-74 cms. and continues to the bottom of the core at 124 cms. Above this the fauna appears to be uniform and of a moderately warm-water nature.

Core 14-38. *Globigerina pachyderma* is common at 73-80 cms. in association with an abundance of warm-water types and does not occur either above or below. This discordance is difficult to interpret with any assurance.

Core 15-38. This shows no suggestion of a cold-water assemblage. The bottom section (176-183 cms.) has a fauna of warmer type than that at the top. Core 19-38 has a consistent fauna which shows some colder aspects at the bottom of the core (165-175 cms.) and probably represents a transition into a colder fauna not reached by this core.

INTERPRETATION OF FAUNAL DATA

GENERAL STATEMENT

The submarine coring done to date by Stetson and whose faunas are here described is largely in the nature of a reconnaissance. This is also true, to a certain extent, of the faunal studies themselves. For these reasons the faunal interpretations are tentative and subject to revision as further study of additional material is made.

The questions raised by Cushman, Henbest, and Lohman (1937, p. 1304) in regard to the efficiency of the coring tube are still pertinent to the interpretations of these faunas and have been discussed in part. Experience with a large number of cores and their microfaunas has led the writer to agree that a comparatively undisturbed section of the bottom is obtained. Some faunal mixing may occur in the upper part of a core taken in extremely soft material, but this need not affect accuracy of

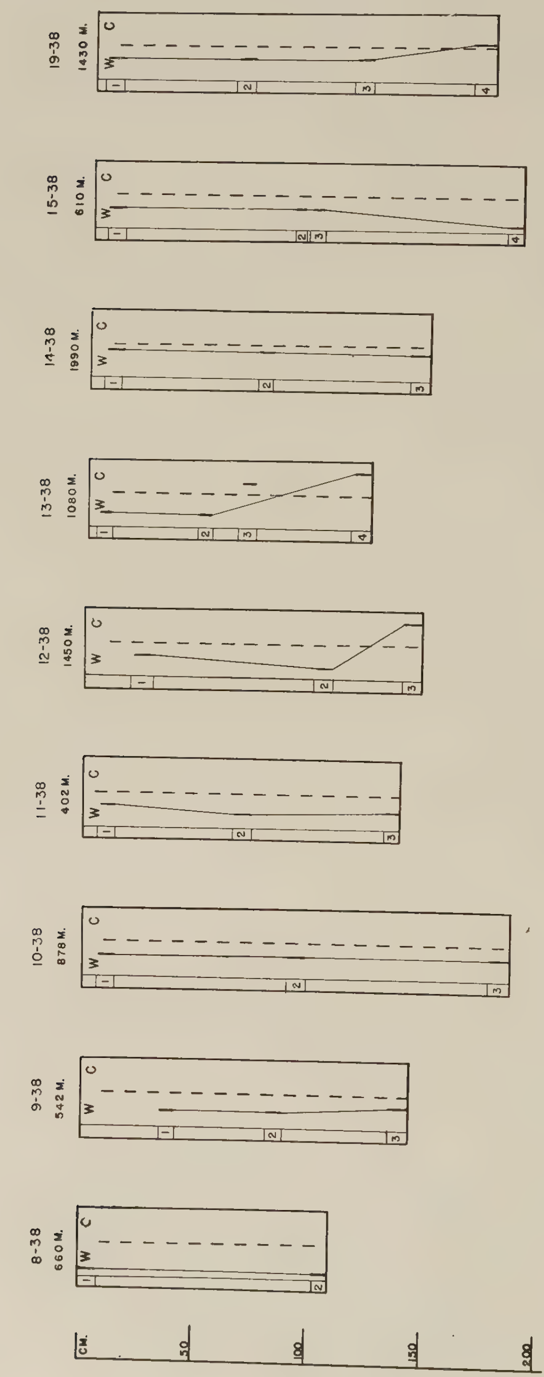


FIGURE 4.—*Relative water temperature indicated by faunas in Chesapeake Bay group of cores*

W = warm water; C = cold water.

sampling because a sample can be taken below this mixed zone. "Whether the fauna in the lower part of the core may have been swept from near shore by currents not now active" (Cushman, *et al.*, 1937) is an important problem which cannot be answered satisfactorily until more evidence is obtained. Such a circumstance would seriously affect the interpretations here offered.

The most important factual contributions of these data are the recognition of one or more Arctic or sub-Arctic faunas beneath the sediments being deposited at the present time and their occurrence over a large area of the continental slope, extending to the western edge of the Atlantic basin.

THE ARCTIC FAUNA

The Arctic type assemblage was without a doubt deposited when the water temperature was much lower than it is at present. At present an assemblage of species is being incorporated into the sediments which is quite characteristic of warm water and in general is similar in type, but not degree, to faunas of tropical waters. The general uniformity of the major aspects of this present-day fauna over all the continental slope samples precludes its accidental introduction by a warm-water current such as the Gulf Stream; it occurs at a considerable distance from the Gulf Stream in many places. It must therefore be considered as typical of these areas of the warm slope water.

The Arctic foraminiferal assemblage, then, is quite foreign to the continental slope at the present time and is characteristic of cooler waters such as in the Arctic and sub-Arctic regions. According to Cushman (1937),

> "the conclusion seems warranted that the material . . . represents a fauna of cold environment, such as that now present within the Arctic Circle."

This statement does not precisely apply to all the assemblages which are here designated as of cold water aspect but it is true of one or more samples beneath the surface in cores 2, 3, 4, 6, 7, 8, 13, 14, 1-38, 3-38, 5-38, 6-38, 12-38, 20-38, 23-38, 13-38, and 22-38. In other cores of the present series and in some samples of the cores listed above the cold-water assemblages do not seem typically Arctic.

The Arctic microfauna is similar to that identified by Cushman from Georges Bank (1936). Several short cores were collected by Stetson (1936) from the bottoms of the three Georges Bank canyons investigated by him. Four of them penetrated the coarse silt on the surface, which contains Recent warm-water Foraminifera, to a fine-grained silt, at a depth of a few centimeters, containing an Arctic assemblage. The locations of the four Georges Bank cores containing the Arctic Foraminifera are as follows: Core 1, N. Lat. 40°23′03″, W. Long. 68°08′, depth 943 meters; core 2, N. Lat. 40° 20′, W. Long. 68°09′, depth 633 meters; core 5, N. Lat. 40°20′40″, W. Long. 67°51′30″, depth 864 meters; core 6, N. Lat. 40°20′40″, W. Long. 67°50′40″, depth 530 meters. Cores 1 and 2 are from the middle of Stetson's canyon I, and cores 5 and 6 are from the middle of his canyon II.

A similar cold-water fauna has been obtained from the basal part of a core (148-164 cms.) taken "about 150 land miles South of New London, Connecticut, and 130 miles East of Atlantic City, New Jersey" at a depth "calculated to be about 2200 meters." (Cushman, *et al.,* 1937). The geographic location is 72° W. Long. 39°13′ N. Lat. In commenting on this lower fauna Cushman (1937, p. 1303) states:

> "The globigerinids belong to species, particularly *Globigerina pachyderma* Ehrenberg, which are known as bottom living forms mostly confined to the Arctic and within the Arctic Circle. With them are species of *Cassidulina, Bulimina, Virgulina, Eponides,* and *Elphidium,* which are characteristic of the Arctic region . . ."

Judging from its vertical position and geographic location, this fauna is undoubtedly to be correlated with the similar one in the present cores.

Several submarine cores were collected by Piggot across the North Atlantic which have been studied by Bradley, Cushman, and others (1937). The complete report of this study is not yet published, but the present writer has been privileged to examine some of the foraminiferal material and data at the Cushman Laboratory, through the generosity of Dr. Cushman. One or more Arctic faunas has been identified from these cores, and the character of this assemblage is similar to that in the present cores. The upper Arctic fauna in the former cores is, in the writer's opinion, to be correlated in time with the upper one in the continental slope cores.

The fact that all the species of the Arctic microfauna are still living indicates that it was deposited at a fairly recent time. It is to be correlated with one or more phases of the Pleistocene ice advance, during which time the oceanic waters must have been considerably cooled, especially near the southern limit of the ice sheet. The Arctic microfauna which occurs directly beneath the Recent, and which is the only one recognized in most of the cores here discussed, probably represents some phase of the Wisconsin stage. In most cases, only the latter part of this stage is certainly shown, since the majority of the cores do not penetrate to the bottom of the upper Arctic fauna.

In Core 14, taken in the Atlantic basin at a depth of 3900 meters, there are two Arctic microfaunas separated by a warm-water fauna. The interpretation of this occurrence presents difficulties because of the vertical distribution of the different types. The upper Arctic material has a thickness of only 7 cms., and the lower material ranges through at least 164 cms.; the warm-water fauna separating these occurrences came from a band only 1 cm. in thickness, and immediately adjoining samples above and below contain a radically different and distinctly cold-water assemblage. It is possible that the two cold-water faunas represent two separate glacial maxima of Wisconsin time, but more faunal data are needed from this area.

According to recent temperature data from the western North Atlantic (Iselin, 1936), the water below a depth of about 800 meters above the continental slope is uniformly cold (about 5° C. or less) and does not have a seasonal variation. The lowered temperature during a time of ice advance would have had most effect upon the surface layers of water, above about 800 meters. The effect upon the deeper water must have been relatively slight since these waters are uniformly cold at the present time, being composed of Arctic water. The ecological significance of the lowered bottom temperature insofar as the Foraminifera are concerned may have been slight since the change probably was relatively small. It would be expected that the near-surface temperature would have been lowest near the ice sheet, with true Arctic surface conditions prevailing much farther south than at present. Under such conditions there would be a zonation similar to that at present, with progressively warmer water away from the ice border. A possible suggestion of such zonation is observed in comparing the Arctic fauna of the more southerly cores with that of the more northerly cores.

In the southerly cores the cold-water fauna differs from the northern fauna, in many cases, in having rare occurrences of typically warm-water pelagic species.

The oceanic circulation also must have been affected by the presence and position of the ice sheet. This would further alter the positions of cold- and warm-water areas other than by a simple zonation away from the ice. The path of the Gulf Stream, for example, must have been somewhat different from its present path. It is possible that study of sufficient additional core material may give some data on this point.

POSTGLACIAL WARM-WATER FAUNA

In six of the present cores an assemblage of Foraminifera occurs beneath the present-day assemblage and above the Arctic fauna which contains a greater abundance of typically warm-water species than in the top sample of the same core. This may be explained as due to accidents of sampling, but since it is rather widespread it appears that such is not the case. Its nonrecognition in other cores may be due to insufficient sampling. This observation has been made in cores 2, 7, 5-38, 7-38, 22-38, and 12-38, and it may be present but not recognized in other cases. The geographic position of these cores ranges from 39°57′ N. Lat. to 37°21′ N. Lat., and from 70°41′ W. Long. to 74°21′ W. Long. Assuming that this observation is not due to unavoidable errors of sampling, it suggests that there existed during some part of postglacial time warmer surface waters than at present overlie these positions on the continental slope. This may represent a local postglacial shift of the Gulf Stream nearer the shore or some other, smaller area of water. Another possibility is that it represents generally warmer surface-water conditions. The Foraminifera concerned in this observation are pelagic types, and therefore the possible interpretations can apply only to the surface-water layers.

In recent peat bog studies in eastern Canada Auer (1930) has collected evidence which points to one warmer postglacial climatic period than at present obtains in that region. This conclusion is based upon pollen analysis and shows that the present spruce forest is a recent development for the area. Sears, in his survey on the use of pollen analysis in dating cultural deposits, states (1937, p. 66) that

> . . . "while the events of early post-glacial climate are still obscure and no doubt confused by irregular edaphic conditions along the retreating ice front, there is fairly clear evidence of the post-glacial warm dry maximum. . . . This hypothesis is not without support from floristic and ecological sources."

The evidence of postglacial warmer faunas in the cores is of sufficient possible significance to merit further investigation. The recognition of warmer postglacial climates on the land is very suggestive in this connection.

PELAGIC AND BENTHONIC TYPES

The species which are characteristic of the Arctic fauna in the cores are usually considered bottom-living types in shallow water, such as *Globigerina pachyderma, Cassidulina, Elphidium, Virgulina,* and *Bulimina* (Cushman, 1937). The occurrence of this assemblage under such circumstances has been used to "indicate considerable changes in sea level" (Cushman, *et al.,* 1937) during the Pleistocene. In view of the far-reaching implications of such a suggestion, particularly as it applies to the hypotheses for origin of submarine canyons, the ecologic information upon which it is based deserves to be examined.

The benthonic nature of *Globigerina pachyderma,* reported by Cushman (1924, p. 15) apparently is based upon Brady's record of it; he found that it occurs "only in bottom dredgings, not in the pelagic gatherings." Murray (1897, p. 20) recorded *G. pachyderma* in the pelagic samples.

> "In the Arctic and Antarctic regions *Globigerina dutertei* and *pachyderma,* together with very minute specimens of *G. bulloides,* appear to be the only forms present in the surface water."

The reliability of *Elphidium* as an indicator of shallow water has recently been questioned by Cushman (1937) since it occurs at several stations in the Pacific at considerable depth (Cushman, 1914, p. 30-34). The genus occurs in the Recent assemblage in nine of the present cores which have a depth range from 402 to 2579 meters. In all but one or two of these occurrences *Elphidium* is rare. The genus is most commonly seen in shallow water, such as on the continental shelf, and some species have been observed living commensally with algae.

Species of *Cassidulina* are rare to common in about half of the Recent samples of the present cores, and the same observation has been made on the species of *Virgulina* most commonly associated in the Arctic assemblages from the cores.

Considering the above facts, it does not seem valid to conclude that the Arctic fauna necessarily indicates any shallower conditions than does the Recent fauna. Relatively little is known about the habits of living Foraminifera, and until a great number of pertinent observations are made it will be difficult to prove details of interpretation based upon depth distribution. The writer is inclined to suspect that more species live in the upper zone of sunlight penetration than have been observed. They may live in association with algae or other things in this zone of maximum life development. The failure to find pelagic types in certain tows whose skeletons are present in bottom gatherings in any region is negative evidence and not necessarily conclusive. In the experience of the men working at the Woods Hole Oceanographic Institution, Foraminifera are only rarely observed in the average plankton tows. This is true even in areas where pelagic forms are known to live in some abundance.

If extensive reworking of deposits has occurred on the continental slope, or if currents not now active carried the shallow-water types out from shallow water and deposited them in deeper water, their occurrence can be easily explained. This is a definite possibility, since the generally lowered sea level obtaining during an ice advance must have redistributed some of the sediments of the upper part of the continental shelf. There is no evidence of wear due to transportation on many of the Foraminifera examined by the author. This is not necessarily a criterion, however, because of the small size of the tests and the lubrication afforded them by being constantly in the water, as commonly observed in washing foraminiferal material. The author is aware of no evidence that reworking of deposits is occurring on a large scale on the deeper parts of the slope at the present time. The distribution of species in the Recent fauna appear to suggest that such is not the case. It must be admitted, however, that some associations in the samples from the cores suggest a possibility of reworking in isolated locations, but this is not a general observation.

CONCLUSIONS

(1) The foraminiferal microfaunas from several submarine cores from the continental slope of the western North Atlantic have been examined and described.

(2) Beneath the Recent fauna there is a widespread Arctic to sub-Arctic assemblage not now living in this region of the continental slope. This is considered Pleistocene, and probably Wisconsin in age, and is to be correlated with Arctic faunas reported from other cores in the western North Atlantic.

(3) Near the edge of the ocean basin two Arctic faunas have been observed, separated by a warm-water fauna. This may represent two ice advances, but the evidence is not conclusive.

(4) In a few cores a fauna of warmer-water aspect than the present one occurs at a short distance beneath the top of the cores. This suggests a possible postglacial shift in warm-water areas.

(5) Indirect evidence suggests that water temperature may be a prime factor in the distribution of Foraminifera. Evidence for considerable change in sea level is considered inadequate.

(6) The conclusions are tentative and will be conditioned by further study of additional core material.

WORKS TO WHICH REFERENCE IS MADE

Auer, V. (1930) *Peat bogs in southeastern Canada,* Geol. Survey Canada, Mem. 162, 32 pages.

Bradley, W. H., *et al.* (1938) *United States Geological Survey's work on the Piggot deep-sea cores* (abstract), Geol. Soc. Am., Pr., p. 71.

Cushman, J. A. (1914) *A monograph of the Foraminifera of the North Pacific Ocean,* Pt. IV, p. 1-46.

——— (1918-1931) *Foraminifera of the Atlantic Ocean,* U. S. Nat. Mus., Bull. 104, 8 parts.

——— (1922) *Foraminifera of the Atlantic Ocean,* U. S. Nat. Mus., Bull. 104, pt. 2, p. 1-109.

——— (1924) *Foraminifera of the Atlantic Ocean,* U. S. Nat. Mus., Bull. 104, pt. 5, p. 1-55.

——— (1936) *Geology and paleontology of the Georges Bank canyons,* Pt. IV, *Cretaceous and Late Tertiary Foraminifera,* Geol. Soc. Am., Bull., vol. 47, pt. 1, p. 413-441.

———, Henbest, L. G., and Lohman, K. E. (1937) *Notes on a core sample from the Atlantic Ocean bottom southeast of New York City,* Geol. Soc. Am., Bull., vol. 48, p. 1297-1306.

Iselin, C. O'D. (1936) *A study of the circulation of the western North Atlantic,* Papers in Physical Oceanography and Meteorology publ. by Mass. Inst. Technol. and Woods Hole Oceanogr. Inst., p. 1-101.

Murray, John (1897) *On the distribution of the pelagic Foraminifera at the surface and on the floor of the ocean,* Nat. Sci., p. 17-27.

Piggot, C. S. (1936) *Apparatus to secure core samples from the ocean bottom,* Geol. Soc. Am., Bull., vol. 47, p. 675-684.

Sears, P. B. (1937) *Pollen analysis as an aid in dating cultural deposits in the United States,* Early Man, p. 61-67, New York.

Stetson, H. C. (1936) *Geology and paleontology of the Georges Bank canyons,* Pt. 1, *Geology,* Geol. Soc. Am., Bull., vol. 47, p. 339-366.

Veatch, A. C., and Smith P. A. (1939) *Submarine valleys of the Atlantic,* Geol. Soc. Am., Spec. Pap. 7 (in press).

AMHERST COLLEGE, AMHERST, MASS.

MANUSCRIPT RECEIVED BY THE SECRETARY OF THE SOCIETY, MARCH 3, 1939.
PRESENTED BEFORE THE GEOLOGICAL SOCIETY, DECEMBER 28, 1938.
CONTRIBUTION NO. 204, WOODS HOLE OCEANOGRAPHIC INSTITUTION.
PROJECT GRANT 238-38.

EXPLANATION OF PLATES

Plate 1

Figure

Species Typical of Warm-water Samples

(1, 2) *Globorotalia menardii* (d'Orbigny). (× 54.) (1) ventral view; (2) dorsal view. Core 11, sample 1.

(3, 4) *Globorotalia hirsuta* (d'Orbigny). (× 54.) (3) ventral view; (4) dorsal view. Core 11, sample 5.

(5, 6, 7) *Globorotalia tumida* (H. B. Brady). (× 54.) (5) ventral view; (6) side view; (7) dorsal view. Core 8, sample 1.

(8) *Globigerinoides conglobata* (H. B. Brady). (× 60.) Core 11, sample 5.

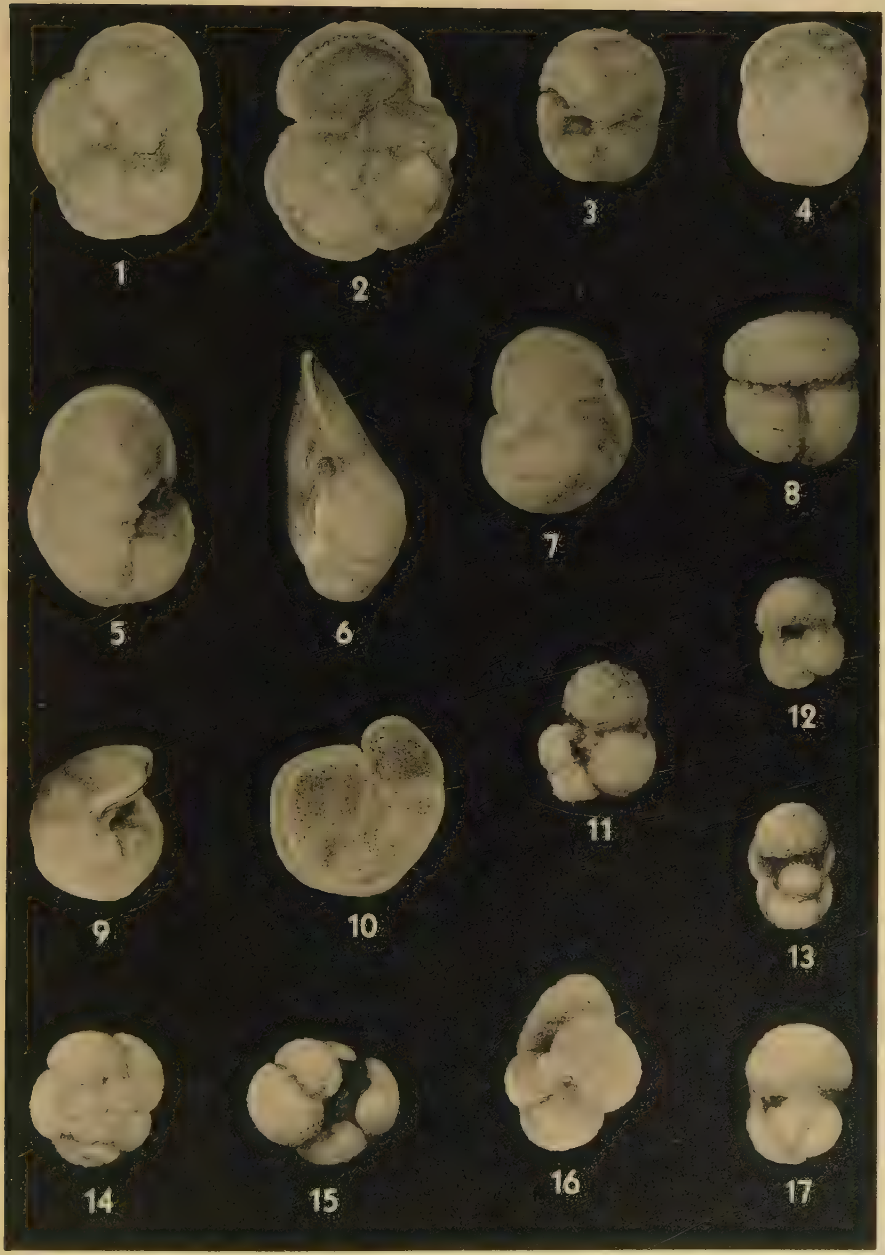
(9, 10) *Globorotalia truncatulinoides* (d'Orbigny). (× 58.) (9) dorsal view; (10) ventral view. Core 11, sample 5.

(11, 13) *Globigerinella aequilateris* (H. B. Brady). (× 60.) (11) side view; (13) apertural view. Core 2, sample 3.

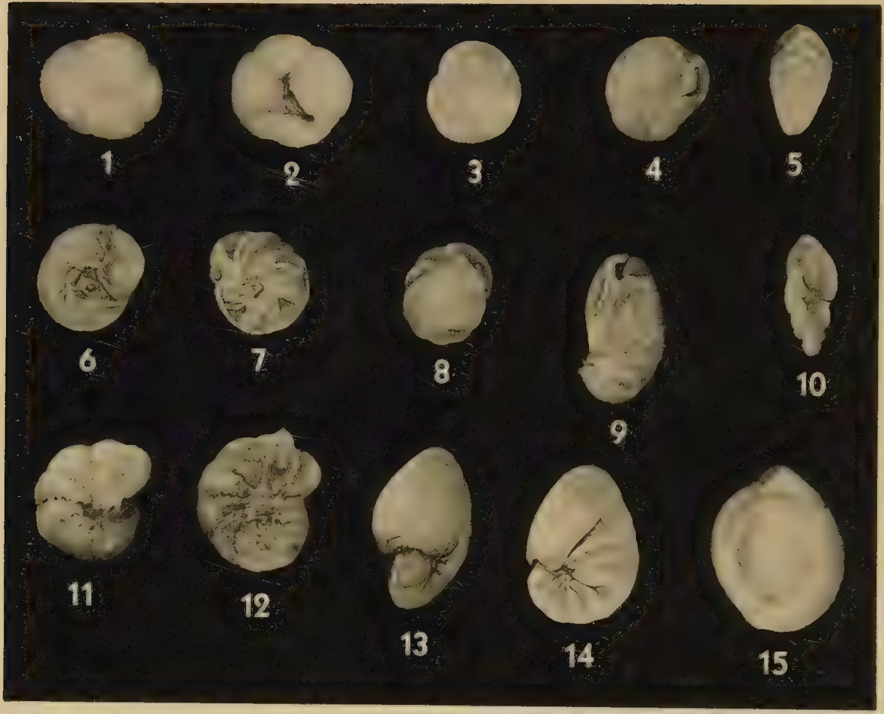
(12) *Globigerinoides rubra* (d'Orbigny). (× 60.) Core 11, sample 5.

(14, 15) *Globigerina dubia* Egger. (× 60.) (14) dorsal view; (15) ventral view. Core 11, sample 1.

(16, 17) *Globigerinoides sacculifera* (H. B. Brady). (× 60.) (16) a specimen showing the projected last chamber; (17) side view of a specimen without the projected last chamber. Core 2, sample 2.


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17

SPECIES TYPICAL OF WARM-WATER SAMPLES


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15

SPECIES TYPICAL OF ARCTIC SAMPLES

PLATE 2

SPECIES TYPICAL OF ARCTIC SAMPLES

Figure

(1, 2) *Globigerina pachyderma* (Ehrenberg). (× 72.) (1) dorsal view; (2) ventral view. Core 3-38, sample 3.

(3, 4) *Cassidulina subglobosa* H. B. Brady. (× 90.) Showing opposite sides. Core 7, sample 5.

(5) *Bolivina* sp. 1. (× 90.) Core 2, sample 2.

(6, 7, 8) *Cassidulina laevigata* d'Orbigny. (× 62.) (6, 7) opposite sides of a flange-keeled form; (8) usual form referred to this species. Core 11, sample 4.

(9) *Cassidulinoides bradyi* (Norman). (× 90.) Core 9-38, sample 3.

(10) *Virgulina* cf. *squammosa* d'Orbigny. (× 100.) Core 2, sample 2.

(11) *Elphidium* sp. (× 54.) Core 11, sample 5.

(12) *Elphidium advenum* var. *margaritaceum* (Cushman). (× 68.) Core 11, sample 3.

(13, 14) *Nonion labradoricum* (Dawson). (× 62.) (13) peripheral view; (14) side view. Core 3-38, sample 3.

(15) *Quinqueloculina seminulum* (Linnaeus). (×68.) Core 15-38, sample 3.

PLATE 3

SPECIES OCCURRING COMMONLY IN BOTH WARM-WATER AND ARCTIC FAUNAS

Figure

(1, 2) *Cibicides pseudoungeriana* (Cushman). (× 62.) (1) dorsal view; (2) ventral view. Core 6-38, sample 1.

(3,4) *Nonion pompiloides* (Fichtel and Moll). (× 65.) (3) side view; (4) apertural view. Core 11, sample 5.

(5, 6) *Uvigerina peregrina* Cushman. (× 60.) Core 3-38, sample 1.

(7, 8) *Nonion* cf. *grateloupi* (D'Orbigny). (× 100.) (7) side view; (8) apertural view. Core 2, sample 1.

(9) *Virgulina schreibersiana* Czyzek. (× 66.) Side view. Core 1, sample 1.

(10, 11) *Angulogerina angulosa* (Williamson). (× 66.) Core 11, sample 5.

(12, 13, 14) *Angulogerina* sp. 1. Core 1-38, sample 1.

(15, 16) *Globigerina bulloides* d'Orbigny. (× 72.) (15) ventral view; (16) dorsal view. Core 11, sample 1.

(17) *Buliminella elegans* var. *exilis* (H. B. Brady). (× 60.) Core 2, sample 1.

(18, 19) *Globigerina inflata* d'Orbigny. (× 60.) (18) ventral view; (19) dorsal view. Core 3-38, sample 1.

(20) *Pyrgo subsphaerica* d'Orbigny. (× 44.) Core 11, sample 5.

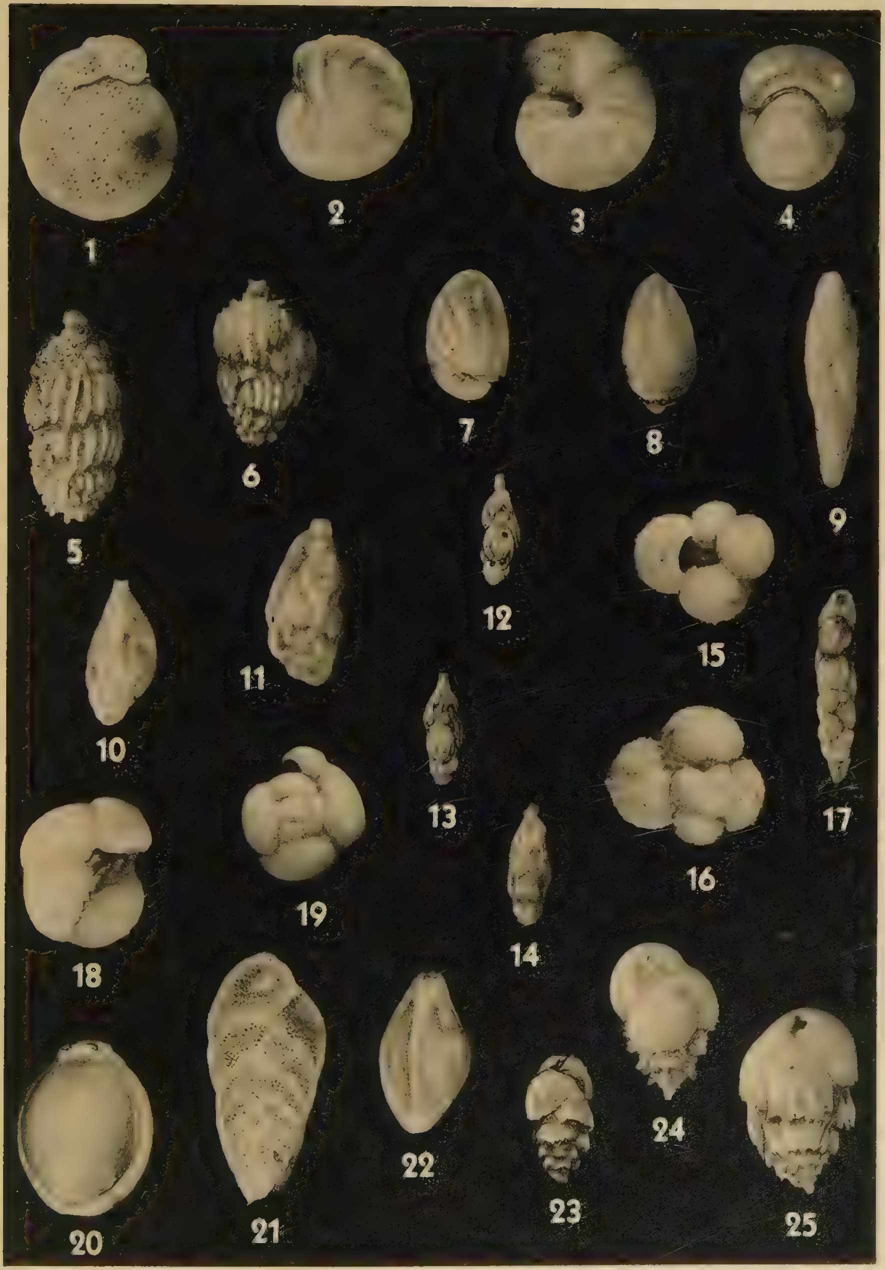
(21) *Bolivina subaenariensis* Cushman. (× 50.) Core 4, sample 3.

(22) *Triloculina tricarinata* d'Orbigny. (× 68.) Core 11, sample 5.

(23) *Bulimina marginata* d'Orbigny. (× 72.) Core 9-38, sample 1.

(24) *Bulimina aculeata* d'Orbigny. (× 54.) Core 11, sample 5.

(25) *Bulimina* cf. *inflata* Sequenza. (× 58.) Core 11, sample 5.


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25

SPECIES OCCURRING COMMONLY IN BOTH WARM-WATER AND ARCTIC FAUNAS

Contribution No. 205

Reprinted from BIOLOGICAL BULLETIN, Vol. LXXVI, No. 2, 256–279, April, 1939
Printed in U. S. A.

DIURNAL VERTICAL MIGRATIONS OF DEEP-WATER PLANKTON

TALBOT H. WATERMAN, RUDOLF F. NUNNEMACHER, FENNER A. CHACE, JR., AND GEORGE L. CLARKE

(*From the Woods Hole Oceanographic Institution*[1] *and the Biological Laboratories, Harvard University*)

INTRODUCTION

Diurnal vertical migrations have long been known to play an important part in the lives of pelagic organisms. The numerous previous studies on these migrations in oceanic animals have been limited almost entirely to plankton living relatively near the surface. It was the purpose of the present investigation to continue and extend the observations made by Welsh, Chace, and Nunnemacher (1937) on the diurnal vertical migrations of deep-water animals. More specifically, our objectives were (1) to ascertain the vertical extent of these migrations for the bathyplankton,[2] (2) to determine the greatest depth in the sea at which these migrations still occur, and (3) to discover the relations of these phenomena to the changes in submarine illumination with time and depth.

HISTORICAL CONSIDERATIONS

The earliest knowledge of diurnal vertical migrations of marine organisms arose from the practical observations of fishermen. Thus man has known from time immemorial that under certain conditions if he wishes to obtain a good catch of herring, his nets should be set deep in the water during the daytime and shallower at night. Such observations were abundantly confirmed and extended for shallow-water animals by the work of a great many marine biologists (an extensive literature is cited by Rose, 1925; Russell, 1927; and Clarke, 1933*b*).

As far as the plankton of deeper water was concerned, a small amount of information was also already at hand by quite an early date. For example Rang (1828) observed that the pteropod, *Hyalocylis striata,* among others, could be taken at the surface of the sea only after sunset and before sunrise and sank into deeper water during the day. Recently Stubbings (1938) has found that this species descends during the day to 200–250 m. so that for at least part of the day it is a bathypelagic organism, i.e., one which lives in the intermediate depths rather than near the surface or the bottom of the sea. But the significance of this and other similar early observations was not appreciated until long afterwards since the existence of a bathyplankton had not been realized until the latter part of the nineteenth century when the data of the various great oceanographic expeditions were analyzed.

---

[1] Contribution No. 205, Woods Hole Oceanographic Institution.

[2] See Ekman ('35, pp. 451–77) for a comprehensive general discussion of the bathypelagic fauna.

Murray (1885, p. 218) concluded from his experiences on the "Challenger" that, "the great majority of plankton organisms live at various depths down to and even deeper than 100 fathoms during the day . . . and only come to the surface at night. . . ." Other investigators came to similar general conclusions (e.g., Chun, 1890, pp. 82–4; Brauer, 1906, p. 337; 1908, p. 232). Brauer was among the first to point out the possible relation of these migrations to such interesting biological problems as bioluminescence, type and size of eye, and pigmentation in the bathyplankton.[3] However, it remained for Fowler (1905, 1909) first to demonstrate by means of numerical data for schizopod and ostracod crustaceans the diurnal vertical migrations of moderately deep-living species. Soon afterwards Murray and Hjort (1912) showed clearly that such migrations were undertaken by organisms which were definitely "deep-sea" animals during the daytime; these investigators also emphasized the correlation of these phenomena with the general biology of the sea, sustaining and extending some of Brauer's suggestions by means of their more complete data.

The further inquiry into the exact and quantitative aspects of the subject presented considerable technical difficulties since for this purpose it is necessary to know accurately where the plankton has been caught, which is impossible when working with open nets. Hence the precise determination of the vertical extent of diurnal migrations and of the various depths at which they occur had to await the development of efficient deep-sea equipment for sampling populations at known depths without contamination from other strata.

Since the invention of the Sigsbee gravitating deep-sea trap (1880) and Palumbo's closing net (Chierchia, 1885, p. 81), many oceanographers have devised such apparatus; yet it was only very recently that reliable equipment has been available for these purposes.

METHODS

The observations were carried out in July, 1937, at "Atlantis" Station 2894 (39° 06′ N., 70° 16′ W.) which is in continental slope water about 300 miles east of Cape May, N. J. This position was chosen for several reasons: (1) The slope water, except for the superficial layers, is relatively free from currents (see Iselin, 1936, p. 11). (2) The station was far enough from both the Gulf Stream and coastal waters to be free of their influence. (3) The water was sufficiently deep to prevent benthonic organisms from confusing the results. (4) Data from the continental side of the Gulf Stream might offer some interesting points for comparison with results previously obtained (Welsh, Chace, and Nunnemacher, 1937) in the far more transparent waters of the Sargasso Sea.

---

[3] For recent investigations of these problems see Welsh and Chace, 1937, 1938.

In order to keep the ship in about the same geographic position the hauls were made in various directions while the work was being done. The maximum deviation from the original station was about 14 miles (see Table I).

TABLE I

Position of the ship at various times while the work was being carried out. The first position in the table is that designated as Station 2894.

Date	Time	Latitude	Longitude
July 18th	10 P.M.	39°06′ N.	70°16′ W.
19th	5 A.M.	38°57′	70°30′
19th	Noon	39°01′	70°30′
20th	Noon	39°06′	70°33′
21st	Noon	39°00′	70°30′
22nd	Noon	38°59′	70°30′

Horizontally hauled closing nets were used, modified from those employed by Leavitt (1935, 1938) as described by Welsh, Chace, and Nunnemacher (1937). These were 2 m. in diameter at the mouth and 9 m. long; the sides were of stramin, 6 threads to the centimeter, with a silk inset, about 20 threads to the centimeter (54 to the inch), in the tail. While the nets were open, the speed of the ship relative to the surface water was kept close to 2 knots. However, the actual speed of each net in relation to the water layer through which it was moving was not known. Since the water at various depths was probably moving at different velocities and possibly even in different directions, the results in such a situation might be very misleading as to the actual population distributions. But in the present case the fact that the hauls were made in various directions precludes the origin of systematic errors from this source. Furthermore, the evidence from the catches for a regular diurnal migration in the various organisms indicates that the relative movements of the water were not of sufficient magnitude to confuse the results.

The depth at which a net was fishing was estimated by means of the trigonometric relation between wire angle and the amount of cable out. At 1,000 m. this estimate was probably accurate within about 10 per cent, being more accurate in shallower and less so in deeper tows.

Thirty-nine catches in a series of 16 hauls were made with the nets fishing for 2 hours at various depths and times throughout more than 2 diurnal cycles. Each entire haul took 4 hours so that 6 were made in a 24-hour period. Tows were made at 100, 200, 400, 600, 800, 1,000 and 1,200 meters, calculated depth, and since the bottom was at 2,860 m., the population thus sampled was purely pelagic. Although the closing nets worked very well in general, 4 of the 39 hauls failed; these are marked in Fig. 1 by asterisks.

Figure 1 represents graphically the times and depths of all the closing net hauls made at this station and shows that various depths were sampled on succeeding days. During the morning of the third day on station a series of tows at 100 and 1,200 m. was begun, but the sea became too rough to continue towing (force 5 on the Beaufort scale) so only one haul was made before work was stopped. In an attempt to fill in the gaps in our series we made tows at appropriate depths at noon and midnight on July 22, i.e., about 36 and 48 hours after the continuous series of hauls had been abandoned.

Throughout the periods when the plankton hauls were being made, a record was kept of the light intensity on deck; furthermore, two series of measurements of submarine illumination were carried out. The same submarine and deck photometer cases were employed and the same procedure followed as previously described by Clarke (1933*a*, 1938*a*).[4] However, the Westinghouse "photox" cells in his apparatus were replaced by emission photoelectric cells of the "photronic" type (manufactured by the Weston Electrical Instrument Corp.) since the former had been found to be somewhat variable. To measure temperature changes, a small thermometer was installed inside the case of the deck photometer, beside the cell, where it could be read through the photometer window by raising the opal glass momentarily. The temperature inside the photometer case during the day was found to vary between a minimum of 19° C. and a maximum of 35° C. Correction factors throughout this temperature range were determined from tests carried out in the laboratory at the end of the cruise, in collaboration with

---

[4] In making these measurements the shadow of the hull is avoided by heaving the ship to with her stern toward the sun and suspending the sea photometer from the end of the mizzen boom (compare criticism by Poole, 1938).

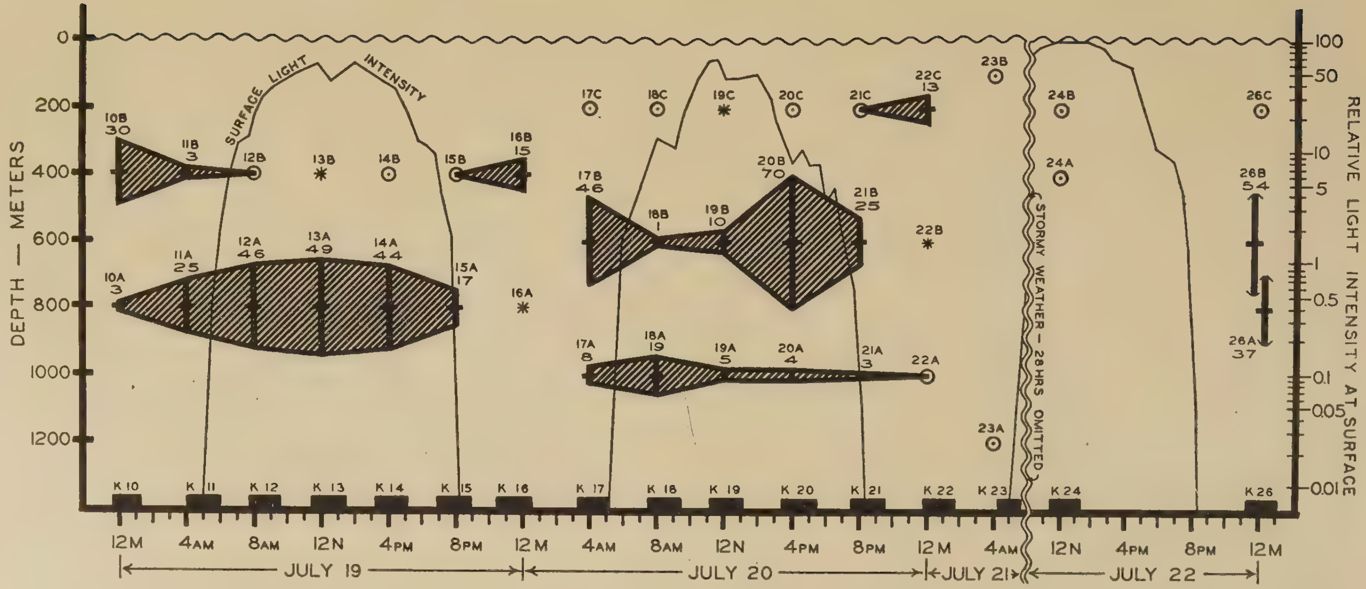


FIG. 1. Distribution in depth and time of the closing net hauls at Station 2894. The numbers of the hauls and their duration are shown by the heavy bars along the time axis. The numbers of the individual nets and their depth are indicated by the small numerals (10*A*, 10*B*, etc.) above the histograms. Those catches which failed are denoted by asterisks. The larger numerals and the vertical bars of the histograms represent the number of adult *Gennadas elegans* taken in each net. Hauls which contained none are designated by an open circle. The changes in the relative surface light intensity are also shown.

Dr. W. R. Sawyer. The proper correction, varying up to a maximum of 12½ per cent, has been applied to each of the photometer readings.

In the first series of measurements of the penetration of light into the water (Series 450) the photronic cell was used with opal diffusing disc, but no filter. Thus the spectral sensitivity of the photometer was that of the photronic cell itself (See Weston Electrical Instrument Corp. Circ. TD–10), the sensitivity of which reached a maximum at 5800 A. and dropped off to 10 per cent of this value at 7080 A. and 3420 A. In the second series (Series 451) the "green" filter combination (Schott-Jena BG–18 and GG–11) used previously and the opal disc were employed. The transmission of this green filter combination exhibited a maximum at about 5100 A. and fell to 10 per cent of this value at about 6460 A. and 4640 A. When these filters were used their selective action was superimposed upon that of the photronic cell with the result that the point of maximum sensitivity of the whole instrument fell between 5800 A. and 5100 A.

Results

This paper presents the results on the occurrence and diurnal vertical migrations of the eleven most numerous malacostracan crustaceans. The decapod, *Gennadas elegans* (Smith), has been chosen for detailed analysis of the data since its presence in significant numbers (526 specimens), its apparent freedom from marked swarming, and its definite diurnal migrations make it a favorable form for our purpose. This prawn was taken at all depths except 100 and 1,200 m. although 83 per cent of the adults captured occurred at 600 and 800 m.

Figure 1 shows that during the first day the number of *Gennadas* present at 800 m. showed a 15-fold increase between midnight and 8 A.M., followed by a further small increase by noon. By 4 P.M. the population present at this depth had decreased to 35 per cent of the number there at noon. Since *Gennadas* disappeared entirely from 400 m. or shallower after 4 A.M. and was not found at this depth again until midnight, the catches strongly suggest that individuals appearing at 800 m. between 4 A.M. and noon had migrated down from lesser depths. The series of hauls at 200, 600, and 1,000 m. on the second day confirmed this indication by showing that the *Gennadas* stock which was present at 200 m. at midnight moved downward a considerable distance during the morning and returned again to shallow water during the afternoon and evening. The numbers taken at 600 m. at various hours of the day suggest further that the bulk of the *Gennadas* stock has gone below 600 m. at the deepest extent of this vertical migration. It is noteworthy that the only hour at which these crustaceans were taken at 200 m. was midnight when a significant number of them were taken at that depth. Clearly a shifting of the population of this species by nearly 400 m. took place on both days when hauls were made.

The conclusions drawn from the above horizontal histograms (Fig. 1) appear even more clearly when the results of the different days are combined and regraphed in the conventional vertical histograms (Fig. 2). It is furthermore apparent from this graph that the vertical spread of the population remained about the same throughout the 24 hours in spite of its bodily translation up and down. Hence these migrations involved a concerted vertical movement of the population as a whole rather than massing and scattering effects due to relative movements between various parts of it.

One of the more striking features of the behavior of the *Gennadas* population shown in Fig. 2 is that the animals were apparently not at the same depths at each midnight. Examination of Fig. 2 shows that the *Gennadas* as a whole are considerably deeper in the water in the second midnight histogram than they are in that for the first midnight. Reference to Fig. 1 demonstrates that the difference between these two histograms depends on the deeper distribution of this prawn on the midnight following the storm of the twenty-first than at the same hour on the preceding days. Specifically, on the midnight of the fourth day none were taken at 200 m. in contrast to the 13 taken there two days before, whereas twelve times as many were taken on this occasion at 800 m. as were taken at the same time and depth four days before.

Our data yield some further details concerning the behavior of *Gennadas elegans*. There were no significant differences in vertical distribution and migration between the males and females (adult). On the other hand, there were notable differences appearing between the behavior of the adult and the post-larval specimens. All of the 67 post-larvae of *Gennadas* taken in our hauls were caught at 600 m.; none appeared at any other depths. Thus, if the post-larvae underwent diurnal migrations, the vertical extent of these was not great enough to bring the animals at any time, in sufficient quantities to be caught, within strata sampled by the other nets.

The evidence at hand for *Hymenodora glacialis* (Buchholz) is unfortunately more circumstantial than conclusive (Fig. 3*A*). Adults were taken only at 1,000 m. and in small numbers; from these facts and from the results of previous work (see Welsh and Chace, 1937, p. 63) it is clear that the adults of *Hymenodora* live generally deeper in the water than our nets fished. The post-larval and immature specimens of this crustacean were living shallower so that a considerable

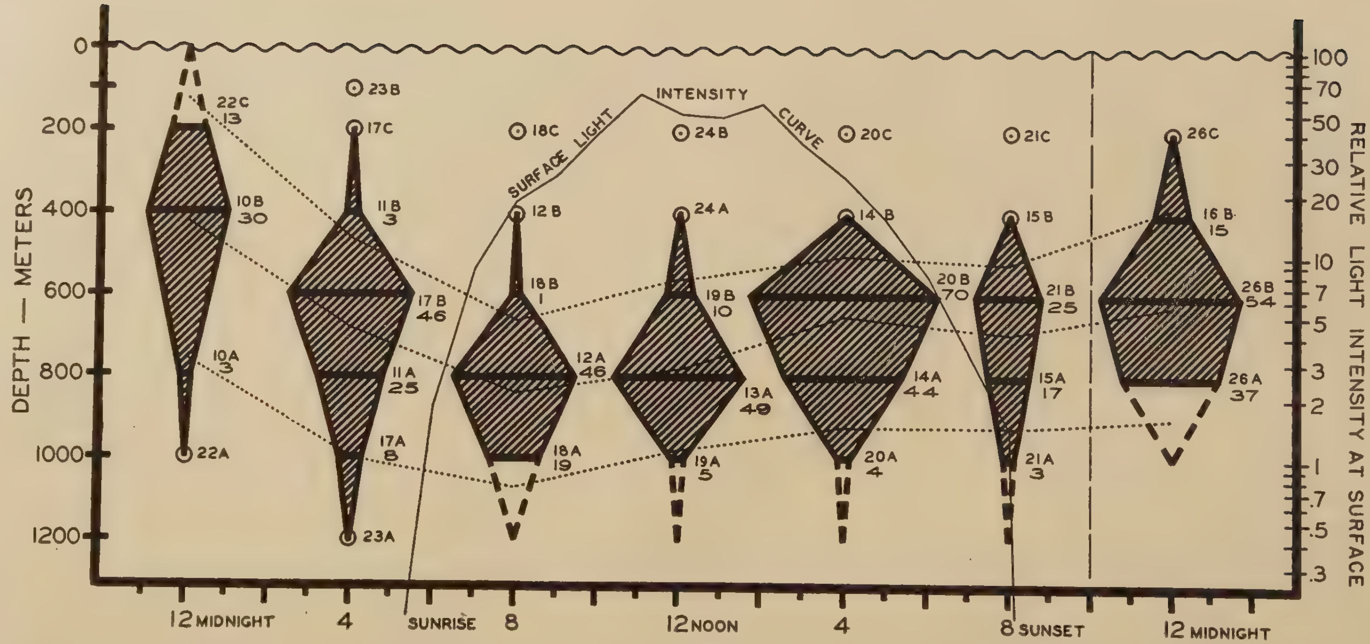


FIG. 2. *Gennadas elegans:* distribution of the adults in the various catches so arranged as to represent the position of the population at the different hours of the day. The small numerals (*22C*, *10B*, etc.) to the right of the histograms are the numbers of the nets, which are given so that the method of combining the data of the different days will be clear from a comparison with Fig. 1. The vertical dashed line separating the second midnight histogram from the rest emphasizes the fact that 3 of the 4 nets in the group were hauled after the storm of July 21. The horizontal bars of the histograms and the larger numerals represent the numbers of animals. The upper and lower dotted lines delimit boundaries of 80 per cent of the population and the middle dotted line represents its center. The light intensity curve is an average for the 4 days measured.

number of them was captured. Sixty per cent of the 153 specimens in the hauls were taken at 1,000 m. and none were caught at any time of day above 800 m. It is unfortunate that the 600 m. net on the midnight of July 20–21 failed to fish so that we do not know whether this prawn was present at this crucial point or not. It we assume on the basis of evidence afforded by some of the other crustaceans, as we have done above for *Gennadas,* that the population was about 200 m. lower in the water on July 22 than on the days preceding the storm of July 21, we can conclude that *Hymenodora* probably was present at 600 m. on the midnight of July 20–21. Owing to the lack of hauls deeper than 1,000 m. during the middle of the day, the lower boundaries of five out of the seven histograms are indeterminate. Indecisive as the present data may be, it is probable, nevertheless, that this animal was undertaking diurnal vertical migrations of about 200 m. amplitude.

Parapasiphaë sulcatifrons Smith (Fig. 3*B*) was the next most numerous decapod crustacean in our catches after *Gennadas* and *Hymenodora.* Fifty-nine per cent of the 123 specimens [5] taken occurred at 800 m. and 10 per cent of them at 1,000 m. Furthermore, this prawn was never caught at 200 m. at any time of day and was taken at 400 m. only at midnight. Thus the general vertical distribution of this species was appreciably deeper in the water than that of *Gennadas* but not of *Hymenodora.*

A diurnal vertical migration of *Parapasiphaë* also occurred. The downward movement was essentially accomplished in the four hours from midnight to 4 A.M. and the upward migration apparently started slowly in the late afternoon although 75 per cent of its extent was accomplished more rapidly after 8 P.M. The fact that these animals, too, were considerably lower in the water on July 22 is shown by the differences between the histograms for the first and second midnights in Fig. 3*B*.

Only one of the six species of *Sergestes, S. arcticus* Kröyer, taken at this station occurred in sufficient numbers for our present purpose. An examination of the distribution in the catches of the 104 specimens of carapace length of 10 mm. or over (Fig. 3*C*) shows that the older stages of this prawn were living shallower in the water than either *Parapasiphaë* or *Gennadas* since the center of the average vertical distribution of the population was just above 600 m. rather than about 800 m. as it was for the other two forms. These *Sergestes,* moreover,

---

[5] Immature, post-larval, and larval specimens were included in this count as well as in the figure. Although the immature specimens were not identified as to species, they were included here as *P. sulcatifrons* since all individuals whose development was sufficiently advanced to permit identification belonged to this species.

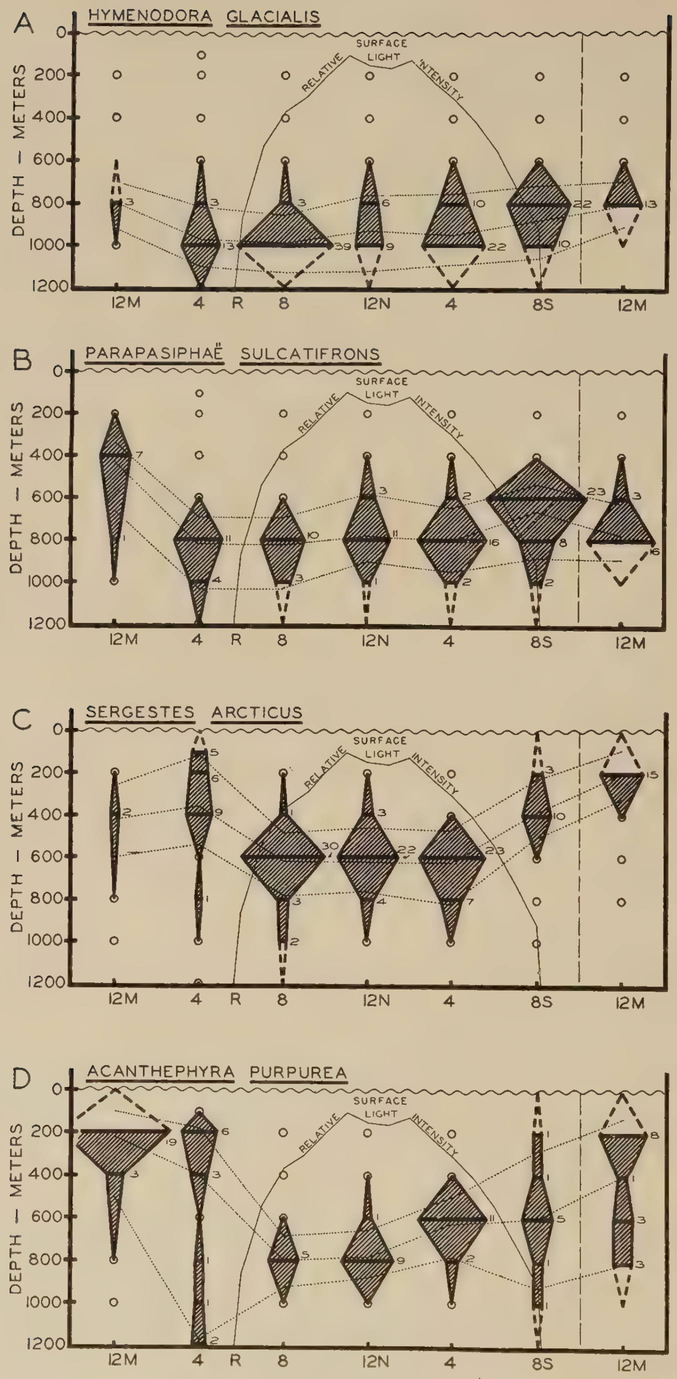


FIG. 3. Decapods: data condensed as in Fig. 2. The numerals to the right of the histograms represent the numbers of specimens taken. These figures include: *A*, larval, post-larval, and immature stages; *B*, all stages; *C* and *D*, adults.

also exhibited an extensive diurnal vertical migration of at least 200 and probably as much as 400 m.

The absence of significant numbers of the species in the hauls made for the first midnight of Fig. 3*C* was probably due to the fact that most of the population was in less than 200 m. of water at this time. Some circumstantial support is given this explanation by the presence of some of these decapods at 100 m. at 4 A.M. and by the position of the population shown by the histogram of the second midnight in Fig. 3*C* since the stock of *Sergestes* by analogy with observations on several of the other Crustacea would be lower in the water by about 200 m. than it would have been at the same time under the conditions of the preceding days.

There is some evidence from an analysis of the catches that those *Sergestes arcticus* of carapace length less than 10 mm. live at and migrate to slightly shallower levels than the larger individuals shown in the figure and discussed above, but hauls closer together than ours would have been necessary to determine this relation quantitatively.

Only 68 *Acanthephyra purpurea* A. Milne-Edwards (Fig. 3*D*) were taken in our hauls, and these had a rather patchy distribution. Nevertheless, there is some definite evidence for the occurrence of a diurnal vertical migration of at least 400 and possibly 600 m.

Among the more primitive malacostracans two species of euphausiïds, two species of mysids, and two species of amphipods were caught in sufficient numbers to provide adequate samples for the present analysis.

The relatively enormous number of 180,000 specimens of the euphausiïd, *Nematoscelis megalops* G. O. Sars (Fig. 4*A*), was taken. The 1,543 adults among these were living mainly between 400 m. and the surface although 12 of them were taken in the only 1,200 m. haul. From the evidence of the very patchy occurrence of all the *Nematoscelis,* one would conclude that this species swarms markedly, which may account for the extremely small numbers caught in the noon hauls. Clearly, however, a diurnal vertical migration at least 200 m. in extent was being accomplished by the adult *Nematoscelis,* shown in the figure.

The other schizopods taken in significant numbers were also migrating vertically, as much perhaps as 600 m. in the case of *Thysanopoda acutifrons* Holt and Tattersall (Fig. 4*B*), and 400 m. in those of the mysids, *Boreomysis microps* G. O. Sars (Fig. 4*C*), and *Eucopia unguiculata* (Willemoës-Suhm) (Fig. 4*D*). A comparison of the histograms of the first and second midnights in Figs. 4*B, C,* and *D,* indicates that these organisms, as well as several of the previously discussed Crustacea, were 200 m. deeper in the water after the storm of July 21

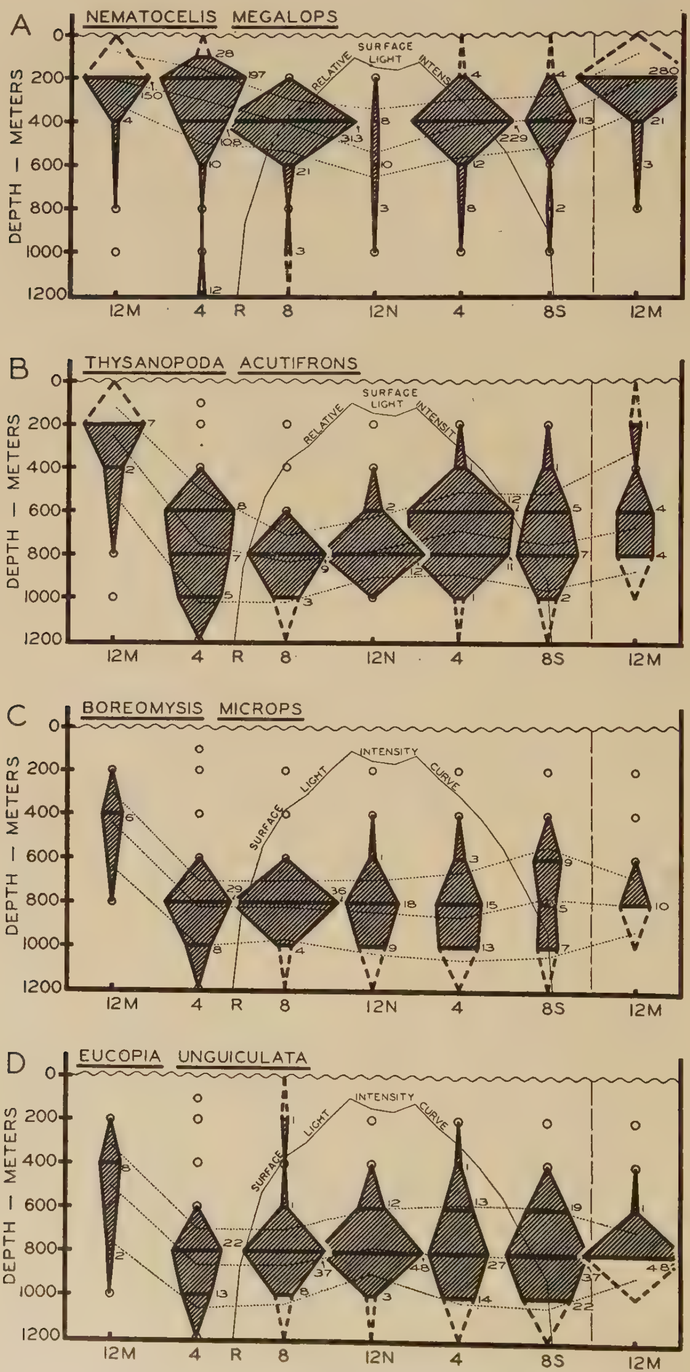


FIG. 4. Euphausiids and mysids. *A*, large adults; *B* and *C*, adults; *D*, all stages. See Fig. 2 for further explanation.

than they were on the previous two days. It is furthermore noteworthy that the *Thysanopoda* (Fig. 4*B*), as well as the *Gennadas* (Fig. 2), *Parapasiphaë* (Fig. 3*A*), and *Acanthephyra* (Fig. 3*D*) apparently began to move slowly upwards in the water almost as soon as they had reached the lowest point of its downward excursion in the morning; this slow upward migration was succeeded at about 8 P.M. by a more rapid movement which brought the animal to the highest point of its migration about midnight.

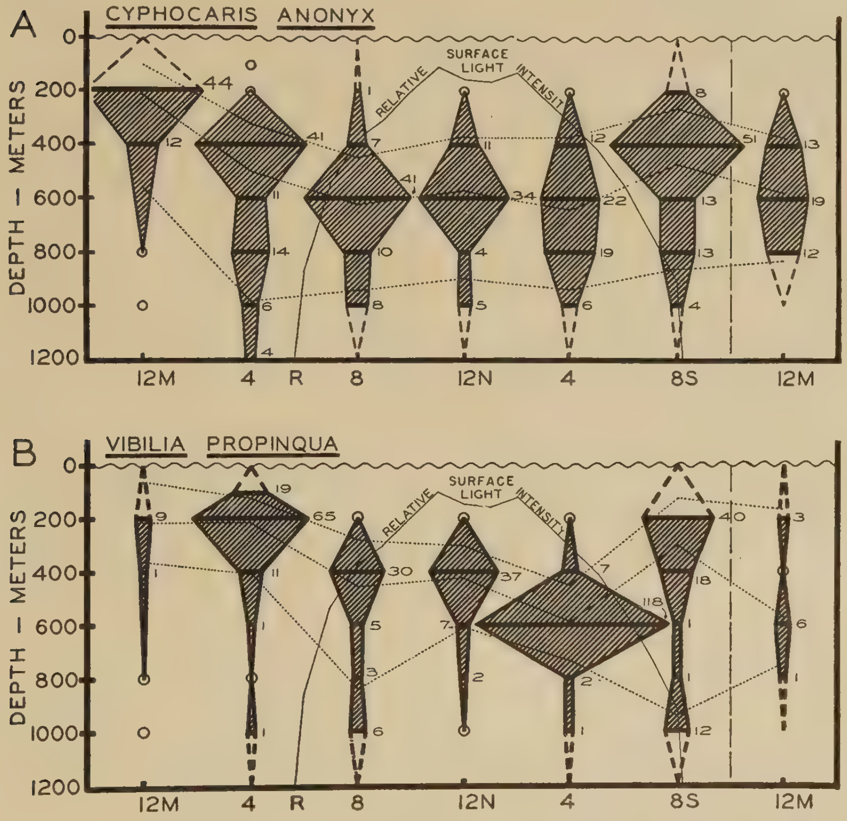


FIG. 5. Amphipods. Adults. See Fig. 2 for further explanation.

The two amphipods caught in sufficient numbers, *Cyphocaris anonyx* Boeck (Fig. 5*A*) and *Vibilia propinqua* Stebbing (Fig. 5*B*), also show a diurnal vertical migration of about 400 m. amplitude. In the case of *Vibilia,* however, the considerable amount of swarming which is apparent obscures this migration somewhat.

DISCUSSION

Since the hauls were made in such a way that our data give us information about points separated in effect by 200 m. and 4 hours, a detailed analysis of the diurnal vertical migrations is clearly impossible. Nevertheless, our results show that all of the crustaceans investigated were accomplishing vertical migrations 200 to 400, and possibly 600 m. in extent, which is in general agreement with the results of recent investigators.

For instance, certain of the larval stages of euphausiids taken by Fraser (1936, p. 154) were apparently moving upward 200–250 m. to reach the surface at night. Stubbings (1938, p. 27) found that species of the pteropods, *Creseis* and *Hyalocylis,* underwent a diurnal migration of 200 m. vertical extent and that some of the other pteropods may have been migrating even further. The copepod, *Pleuromamma robusta,* was shown by Mackintosh (1934, p. 92) to exhibit the most pronounced vertical migration of all the plankton animals of the antarctic surface waters; this crustacean rose into the upper 100 m. around midnight and descended apparently below 600 m. during the day. Among the malacostracan crustaceans Hardy and Gunther (1935, p. 240) observed that *Euphausia frigida* and *E. triacantha* underwent a diurnal vertical migration of at least 200 m. and that the amphipod, *Parathemisto gaudichaudi,* migrated a vertical distance of about 60 m. in the course of its diurnal movement. Since the latter animal was taken within the upper 100 m. at all hours, this observation is similar to those made on other shallow water plankton. Clarke (1934a, Figs. 2 and 3), for example, showed that *Calanus finmarchicus* adults and copepodid stages IV and V exhibited a diurnal migration of about 100 m.

The rate of the diurnal vertical migrations may be roughly calculated from our results. If the speeds of downward movement of the centers of the populations for the various species, as shown in the figures, are taken to represent the average rates of movement for the organisms concerned, these are found to vary from 29 m. per hour for *Nematoscelis* to 125 m. per hour for *Thysanopoda.* The average for the eleven species of crustaceans is 67 m. per hour. The only comparable data are those of Hardy and Gunther (1935, p. 240) mentioned above for the migration of the two species of *Euphausia* in which the upward migration apparently occurred at a rate of 100–200 m. per hour.

In some of these organisms a slower upward movement during the day preceded the more rapid upward migration shortly before midnight. This phenomenon has been observed in shallow-water zoöplankton by a number of workers and has been explained on the basis of a gradual light adaptation of the animals (see Russell, 1931, p. 402; Kikuchi, 1938, p. 37). In spite of this slow upward trend, however, our observations suggest that the upward migration in the early evening hours was as rapid as the downward movement in the early morning.

A comparison of the swimming speeds of the animals in the plankton with the rates of these diurnal vertical migrations would be of great interest. Unfortunately, there are no data available for these or comparable plankton organisms. Measurements have been made, however, of the rates of locomotion of several copepods and crustacean larvae (Russell, 1927, p. 221; Welsh, 1933). The latter found that *Centropages* would swim towards a light of an intensity that might be found 20–30 m. below the surface on a clear day at a rate of 82 m. per hour (actually measured over a path only 10 cm. long). As Parker (1902), Gardiner (1933), and Seiwell and Seiwell (1938) have shown, gravity alone causes copepods to sink at a rate of about 24 m. per hour.

Thus, if any organism to which the above quoted rate of sinking is applicable were migrating downward 400 m. in 8 hours, it would sink 192 m. merely through the effect of gravity and would have to swim downward through the remaining 208 m. at an average rate of 26 m. per hour. For the upward trip the gravitational effect would add the 192 m. to the distance to be swum (see Clarke, 1934*b*) so that the animal would have, in effect, to swim upward at a rate of 592 m. in 8 hours or 74 m. per hour. To consider it in another way, the organism in order to accomplish the downward migration would have to be actively swimming towards the bottom at the experimentally determined rate of 82 m. per hour for only about one-third of the 8-hour period, whereas in order to move upward to the original level in the same length of time it would have to be swimming towards the surface at this rate during 7 of the 8 hours.

As the pelagic malacostracans such as those discussed in this paper are known to be very active swimmers, they could presumably accomplish such vertical migrations with greater ease than the animal postulated above on the basis of data obtained from copepods. The Crustacea in our analysis are larger, moreover, and, other things being equal, would sink more rapidly through the water than the copepods so that an even greater proportion of their downward movement may be effected by the mere absence of any persistently oriented swimming activity. Many experiments have shown that several environmental variables, such as light and temperature, will affect the locomotor activity of zoöplankton, but, as Clarke (1934*b*) pointed out, these factors under natural conditions would seem to work in the wrong direction to explain distribution as it is found.

Since the great majority of previous workers have recognized that light is the most significant single environmental factor in diurnal vertical migrations, it is interesting to correlate these phenomena with the changes in the intensity of illumination at various hours of the day (Fig. 1). During the first hour after daylight became measurable, its intensity increased at an exceedingly rapid rate. Similarly, the illumination diminished at an equally rapid rate during the hour preceding the last measurement of the day. During the four hours in the middle of the day the illumination remained relatively constant and such changes in intensity as resulted from different degrees of cloudiness were of a much lower magnitude than those of early morning and late afternoon.

The most striking point which appears in a comparison of the biological and the light intensity data is that much of the migration apparently occurred when there was no light more intense than starlight even at the surface. Before sunrise most of the animals had already descended about half of their total downward distance, and several, such as *Boreomysis, Eucopia,* and *Parapasiphaë,* had reached the deepest point in their migration by sunrise. In most cases, furthermore, the greater part of the upward migration must have been accomplished between the time of sunset and midnight.

It is clear from these facts that the vertical migrations of these organisms cannot be explained simply on the basis of a negative phototropism which overshadowed a negative geotropism in the daytime and left it with a free hand at night.

Similarly the hypothesis that the animals aggregate by means of a tropistic mechanism (Michael, 1911; Russell, 1934) in a region of optimum light intensity and follow the latter as it moves vertically at various hours of the day apparently will not explain the situation here. Such an hypothesis is further weakened by the lack of evidence in the present case for a general vertical scattering of the population throughout the water column at night when it would be free of the concentrating effect of light.

Whether we assume that external environmental or internal physiological factors are controlling the diurnal migrations, the intensity of illumination penetrating from the surface must play an important rôle in these phenomena since it is the only daily environmental variable in deep water. It may act in combination with other external factors, such as temperature and gravity, since many investigators have shown experimentally that interactions of such factors may cause a tropistic reversal (Kikuchi, 1938, pp. 35–6). Or it may merely keep in phase cyclic internal physiological conditions of the organisms which themselves regulate these migrations (see Russell, 1927, p. 225; Welsh, Chace, and Nunnemacher, 1937, p. 195). Many cases are known (Welsh, 1938, p. 136) of the persistence of internal diurnal rhythms under constant external conditions, but one would expect that in nature at least an occasional action of the external factor to which it owes its origin, in this case light, would be necessary to maintain the synchrony indefinitely.

A second problem is posed by the fact that most of the Crustacea here considered were about 200 m. lower in the water on the midnight of July 22 than they were at the same hour two or three days before. Furthermore, the maximum illumination at the surface on July 22 was 66 per cent greater than the maximum on July 19. Previous studies have shown that certain organisms appear to live at depths where the light intensity is of a particular magnitude, i.e., an optimum intensity for the organism in question; these organisms may, as a consequence, appear in shallower waters on dull days or in high latitudes (Russell, 1933, p. 569; Murray and Hjort, 1912, p. 664–6); thus the light intensity itself may have been responsible for the observed difference in distribution.

It is clear, however, that the amount of illumination could not explain so great a change in distribution. Since actual measurements down to 84 m. (Fig. 6) showed that the light is reduced by a factor of 10, for every 25 m. of water, the observed change in light intensity at the surface would result in a difference of only about 5.5 m. in the depth at which any given intensity of light would be found. Even in the clearest sea water yet measured (see below) this change in light intensity at the surface would result in a maximum change of only 50 m. in the depth to which any particular intensity of light would penetrate.

An alternative causal or contributory factor to the observed lower position of the plankton on July 22 may have been the storm of the previous day, but it is not likely that a relatively mild disturbance of this sort at the surface would be appreciable at a depth of over 200 m. Furthermore, Hardy and Gunther (1935, p. 268) conclude from their observations that, "... the state of the sea has little or no bearing on the number of organisms in the surface layers. . . ."

A more important point is the fact that simultaneous measurements on the horizontal patchiness of the plankton were not made. Consequently we cannot tell whether or not the observed difference might rather be due to the fact that on the later day we were sampling a different population with a different vertical distribution pattern from that of the previous days (Russell, 1933, p. 569; Hardy, 1936).

One of the most important questions raised by previous work on the diurnal vertical migrations of bathypelagic organisms is how deep down in the water do such migrations occur. Most of the crustaceans showing diurnal vertical migrations discussed in this paper were living at depths of 600–800 m. during the four hours during the middle of the day. If, as pointed out above, we recognize the necessity of light in one way or another for the vertical migrations of these animals, we must assume that at some time during the day the organism is affected by light. Clearly, under any given physiological conditions, there is a minimum intensity of illumination which would be just sufficient to affect any particular animal; in the open sea there would be a definite maximum depth beyond which this minimum light intensity would never penetrate even at noon on the brightest days. A diurnal vertical migration in which illumination from the surface was supposed to have any

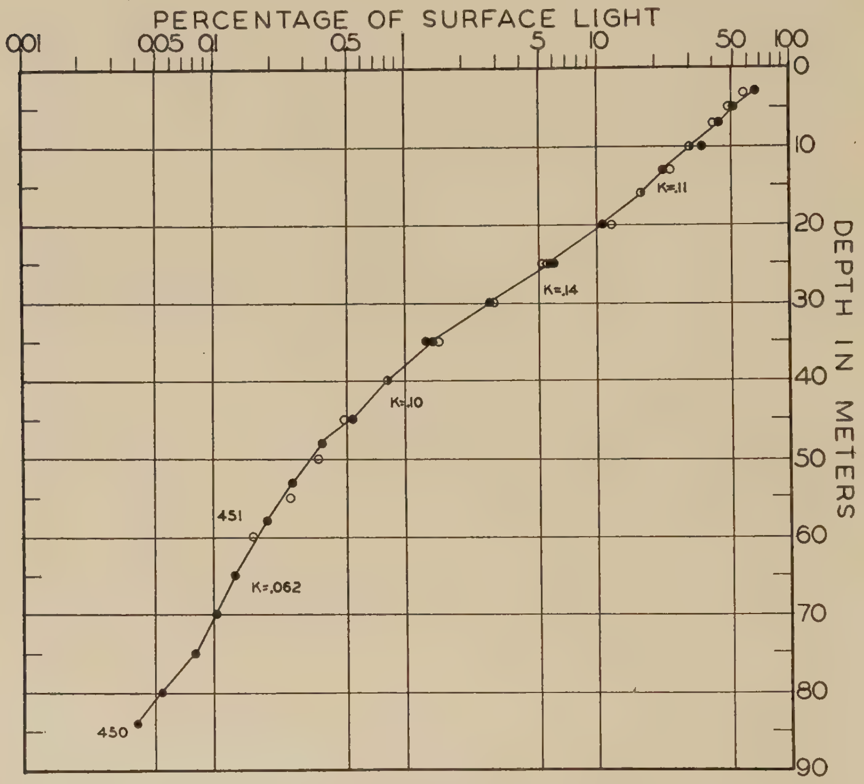


Fig. 6. Relation between depth and irradiation expressed as a percentage of the light just over the surface (logarithmic scale). Station 2894. Lat., 39° 06′ N.; Long., 70° 16′ W. July 22, 1937. Sky: clear. Sea: moderate, white caps. Series 450 measured by photronic cell with opal disc. Series 451 measured by photronic cell with "green" filter combination (Schott-Jena BG–18 and GG–11) and opal disc.

controlling effect would thus be impossible below this depth. As pointed out above, however, vertical migrations could be temporarily maintained under constant conditions by a diurnal physiological rhythm within the organism. Thus, if unusual conditions such as a storm should cut down the incident light so that deep-living animals did not come under the influence of light for several days, there would not be a wholesale loss of the population through continued downward migration or random scattering into unusually great depths (see Russell, 1930), but the diurnal migrations would continue more or less as usual under the guidance of the physiological rhythm.

In view of these facts the question of how much light penetrates to the depths at which the migrating Crustacea are living during the daylight hours is one of great interest. The results of our two series of light penetration measurements, shown in Fig. 6, indicate that the transparency of the water was relatively uniform down to 84 m., the limit of measurement, with an average value of the extinction coefficient[6] of $k = 0.092$ for the green component of daylight. Hence, the intensity of illumination was reduced to one-tenth its value by passage through 25 m. of water. Assuming that the transparency of the water remained the same below the depth of our deepest measurement and extrapolating we find that the illumination at 800 m. would be 10^{-32} times its intensity at the surface.

But if we assume that the water below 100 m. is as clear as any sea water which has been measured, we may on this basis calculate the maximum amount of light possible at any depth. Since the extinction coefficient varies enormously with wave-length, the actual result reached will depend on the part of the spectrum considered. In the clearest water yet known the intensity of light in the green wave-lengths (Clarke, 1938*b*) was reduced to one-tenth by 61 m. of water. Thus if the water below 100 m. at our station was as clear as this, at 800 m. the intensity of illumination would be 10^{-15} times the value at the surface. In the clearest water yet known the blue wave-lengths were reduced to one-tenth their intensity in 230 m. (Clarke, 1933*a*).[7] If water of like transparency existed below 100 m. at our station, the illumination of 800 m. would be a little less than 10^{-7} times the surface intensity;[8] this value is between 100 and 1,000 times higher than the threshold intensity for human vision.

---

[6] In the equation $I/I_0 = e^{-kL}$, where L is the thickness of the water layer in meters through which the intensity is reduced from I_0 to I.

[7] Basing our calculations on the most transparent strata only.

[8] Assuming the same reductions in the upper 100 m. for the blue component as for the green, which is known (Oster and Clarke, 1935) to be approximately true in this region of the Atlantic.

We have some evidence, however, that conditions as favorable for penetration as this latter case for blue light did not exist at our slope water station since on a bright, calm day Beebe (1934, p. 276) observed through the window of the bathysphere that at a depth of 610 m., the water appeared absolutely dark to the human eye. But Beebe was not able to look upward in the water so that he could not tell at what depth the downward component of the light had become indistinguishable from the blackness below.[9] On the other hand, the water of the Sargasso Sea, where Beebe made his observations, is characteristically (Clarke, 1936*a*) nearly twice as transparent in the upper 100 m. for the green region of the spectrum as was the water at our present station.

It would be of great interest to compare the amounts of light present at 800 m., where migrations were definitely going on, with the visual sensitivity of these Crustacea. Unfortunately, no experimental studies have yet been made on vision in any deep-sea animals. Nevertheless, from previous work on crustaceans and other arthropods with compound eyes, it is possible to draw two extremely general conclusions: first, that arthropods are more sensitive to the blue wave-lengths of light than to the green (see Waterman, 1937, p. 464 for table summarizing pertinent data) and second, that for these organisms the minimal light intensity for response is of the order of magnitude of 10^{-6} to 10^{-7} millilamberts (Crozier, 1938, personal communication).[10]

An intensity of illumination of 10^{-6} millilamberts is equivalent to about 10^{-10} times that of full noon sunlight and is the value used by Clarke (1936*b*) as a threshold intensity for determining the depth at which fish can see. A crustacean with a visual threshold of such a magnitude in the green wave-lengths certainly could not be stimulated by this region of the spectrum when the intensity of the latter is reduced to 10^{-15} times that at the surface. Since this would be the illumination present at 800 m., when we assume that the water below 100 m. was as clear as any sea water that has been observed, we may conclude that under these conditions the crustaceans could not be responding to light from the surface. But if the crustacean had an equally low visual threshold for blue light, our calculations have shown that in the clearest water observed there would be almost 1,000 times as much light present at 800 m. as would be necessary for the threshold of vision. Under such maximum conditions even at 1,000 m., where the immature *Hymenodora* in our catches possibly gave some indications of a diurnal vertical migration, more than 100 times the necessary amount of light would be present. The threshold intensity for vision, 10^{-10} of full sunlight intensity, would occur at a depth of nearly 1,500 m. under such conditions.

---

[9] Presumably this directional effect would still be appreciable at great depths since directional differences in intensity were recorded photographically by Helland-Hansen (Murray and Hjort, 1912, p. 252) at 500 m. and since more recent work of Whitney (1938, p. 211) has demonstrated that in optically homogeneous waters the ratio of the intensities of light passing downward to those of the light scattered upward is a constant (see also Pettersson, 1938). Of interest in this connection is the occurrence of upwardly (dorsally) directed "telescopic" and stalked eyes in a number of different families of deep-sea fishes of the "twilight zone" of the seas (Brauer, 1908, p. 233) which would suggest that this directional difference in the light intensities is of biological significance even at considerable depths.

[10] Any value obtained for a sensory threshold will, of course, depend largely on the exact experimental conditions under which it was determined.

Thus, the water below the surface layers could be, as it probably was, considerably less transparent than the clearest sea water ever observed and still permit sufficient visible light for affecting the reactions of bathypelagic organisms to penetrate to depths of about 800 m.

The preceding discussion makes it clear that several important aspects of this problem must be investigated more thoroughly before a satisfactory solution will be possible. These are in brief: (1) actual measurements of the transparency of the water at greater depths and of the relative intensities of the light in various directions; (2) more detailed work on the maximum depth at which diurnal vertical migrations occur; (3) measurements of the photosensitivity of deep-sea animals and correlations of the maximum wave-length sensitivity to the wave-length of the most penetrating part of the spectrum; (4) experimental studies on deep-sea animals designed to elucidate the nature of any diurnal physiological rhythms and their relation to the organisms' behavior in the sea.

SUMMARY

1. A study was made with the aid of closing nets of the diurnal vertical migrations of bathypelagic organisms at a station in continental slope water of the western North Atlantic.

2. While the hauls were being made a continuous record of the light intensity at the surface was kept.

3. The penetration of light into the upper 84 m. of water was directly measured photometrically; the average extinction coefficient for green light was $k = 0.092$.

4. All of the malacostracan Crustacea (to which the detailed results presented in this paper are limited) which occurred in sufficient numbers for analysis exhibited diurnal migrations 200 to possibly 600 m. in vertical extent.

5. The speed of vertical movement in these migrations varied from 24 to 125 m. per hour among the various crustaceans.

6. A considerable part of the migrations took place while the light intensity even at the surface was no greater than starlight.

7. Several Crustacea living at 800 m. during the day showed extensive diurnal vertical migrations.

8. It is concluded, however, that whether the migrations are regulated by external environmental or by internal physiological factors, at some time of day the organisms concerned are affected by light penetrating from the surface.

9. Calculations made from the light penetration data indicate that the amount of light probably present during the middle of the day at the depths where the animals were migrating was adequate to support this conclusion (8).

LITERATURE CITED

Beebe, W., 1934. Half Mile Down. Harcourt, Brace. New York.

Brauer, A., 1906. Die Tiefsee-Fische. I. Systematischer Teil. *Wiss. Erg. Deutschen Tiefsee-Exp. . . . " Valdivia,"* Bd. 15, Lief. 1.

Brauer, A., 1908. Die Tiefsee-Fische. II. Anatomischer Teil. *Ibid.*, Bd. 15, Lief. 2.

Chierchia, G., 1885. Collezioni per studi di scienze naturali fatti . . . dalla . . . " Vettor Pisani." *Riv. Marittima,* Sept. 1885.

Chun, C., 1890. Die pelagische Thierwelt in grossen Meerestiefen. *Verhandl. Gesell. Deut. Naturf. u. Aerzte,* **63** (Pt. 1) : 69–85.

Clarke, G. L., 1933*a*. Observations on the penetration of daylight into mid-Atlantic and coastal waters. *Biol. Bull.,* **65**: 317–37.

Clarke, G. L., 1933*b*. Diurnal migration of plankton in the Gulf of Maine and its correlation with changes in submarine irradiation. *Ibid.,* **65**: 402–436.

Clarke, G. L., 1934*a*. Further observations on the diurnal migration of copepods in the Gulf of Maine. *Ibid.,* **67**: 432–55.

Clarke, G. L., 1934*b*. Factors affecting the vertical distribution of copepods. *Ecol. Monogr.,* **4**: 530–40.

Clarke, G. L., 1936*a*. Light penetration in the western North Atlantic and its application to biological problems. *Rapp. et Procès-verb. Con. Perm. Int. Expl. Mer,* **101** (Pt. 2, No. 3) : 3–14.

Clarke, G. L., 1936*b*. On the depth at which fish can see. *Ecol.,* **17**: 452-6.

Clarke, G. L., 1938*a*. Seasonal changes in the intensity of submarine illumination off Woods Hole. *Ibid.,* **19**: 89–106.

Clarke, G. L., 1938*b*. Light penetration in the Caribbean Sea and in the Gulf of Mexico. *Jour. Mar. Res.,* **1**: 85–94.

Ekman, S., 1935. Tiergeographie des Meeres. Akademische Verlagsgesellschaft. Leipzig.

Fowler, G. H., 1905. Appendix on the vertical distribution and movement of the Schizopoda. *Trans. Linn. Soc. Lond.,* Ser. 2, **10**: 122–9.

Fowler, G. H., 1909. Biscayan plankton collected during a cruise of H.M.S. " Research," 1900. Pt. 12: The Ostracoda. *Ibid.*: 219–336

Fraser, F. C., 1936. On the development and distribution of the young stages of krill (Euphausia superba). *Discov. Reports,* **14**: 1–192.

Gardiner, A. C., 1933. Vertical distribution in Calanus finmarchicus. *Jour. Mar. Biol. Ass'n,* N.S., **18**: 575–610.

Hardy, A. C., 1936. Observations on the uneven distribution of oceanic plankton. *Discov. Reports,* **11**: 511–38.

HARDY, A. C., AND E. R. GUNTHER, 1935. The plankton of the South Georgia whaling grounds and adjacent waters, 1926–1927. *Ibid.*, **11**: 1–456.

ISELIN, C. O'D., 1936. A study of the circulation of the western North Atlantic. *Papers in phys. oceanogr. and meteorol. Mass. Inst. Tech., Woods Hole Oceanogr. Inst.*, **4** (No. 4): 1–101.

KIKUCHI, K., 1938. Studies on the vertical distribution of the plankton Crustacea. II. The reversal of phototropic and geotropic signs of the plankton Crustacea with reference to vertical movement. *Rec. Oceanogr. Works in Japan*, **10**: 17–41.

LEAVITT, B. B., 1935. A quantitative study of the vertical distribution of the larger zoöplankton in deep water. *Biol. Bull.*, **68**: 115–30.

LEAVITT, B. B., 1938. The quantitative vertical distribution of macrozoöplankton in the Atlantic Ocean basin. *Ibid.*, **74**: 376–394.

MACKINTOSH, N. A., 1934. Distribution of the macroplankton in the Atlantic sector of the Antarctic. *Discov. Reports*, **9**: 65–160.

MICHAEL, E. L., 1911. Classification and vertical distribution of the Chaetognatha of the San Diego region. *Univ. Calif. Publ. Zoöl.*, **8**: 21–186.

MURRAY, J., 1885. In *Reports of the "Challenger" Exped.* Vol. 1, Narrative of the Voyage, p. 218.

MURRAY, J., AND J. HJORT, 1912. The Depths of the Ocean. Macmillan Co. London.

OSTER, R. H., AND G. L. CLARKE, 1935. The penetration of the red, green, and violet components of daylight into Atlantic waters. *Jour. Opt. Soc. Amer.*, **25**: 84–91.

PARKER, G. H., 1902. The reactions of copepods to various stimuli, and the bearing of this on daily depth migrations. *Bull. U. S. Fish. Comm. 1901*, **21**: 103–23.

PETTERSSON, H., 1938. Measurements of the angular distribution of submarine light. *Rapp. et Procès-verb. Con. Perm. Int. Expl. Mer*, **108** (Pt. 2, No. 2): 9–12.

POOLE, H. H., 1938. Review of W. M. Powell and G. L. Clarke, 1936. *Jour. Con. Perm. Int. Expl. Mer*, **13**: 111–3.

RANG, M., 1828. Notice sur quelques Mollusques nouveaux appartenant au genre Cléodore, et établissement et monographie du sous-genre Créseis. *Ann. des Sci. Nat.*, **13**: 302–19.

ROSE, M., 1925. Contribution à l'étude de la biologie du plankton; le problème des migrations verticales journalières. *Arch. Zoöl. Expér. Gén.*, **64**: 387–542.

RUSSELL, F. S., 1927. The vertical distribution of plankton in the sea. *Biol. Rev.*, **2**: 213–62.

RUSSELL, F. S., 1930. Do oceanic plankton animals lose themselves? *Nature*, **125**: 17.

RUSSELL, F. S., 1931. The vertical distribution of marine macroplankton. X. Notes on the behaviour of Sagitta in the Plymouth area. *Jour. Mar. Biol. Ass'n*, N.S., **17**: 391–414.

RUSSELL, F. S., 1933. On the biology of Sagitta. IV. Observations on the natural history of Sagitta elegans Verrill and Sagitta setosa J. Müller in the Plymouth area. *Ibid.*, **18**: 559–74.

RUSSELL, F. S., 1934. The vertical distribution of marine macroplankton. *Ibid.*, **19**: 569–84.

SEIWELL, H. R., AND G. E. SEIWELL, 1938. The sinking of decomposing plankton in sea water and its relationship to oxygen consumption and phosphorus liberation. *Proc. Amer. Phil. Soc.*, **78**: 465–81.

SIGSBEE, C. D., 1880. Description of a gravitating trap for obtaining specimens of animal life from intermediate ocean-depths. *Bull. Mus. Comp. Zoöl.*, **6**: 155–8.

STUBBINGS, H. G., 1938. Pteropoda. *John Murray Exp. Sci. Rep.*, **5**: 15–33.

WATERMAN, T. H., 1937. The relative effectiveness of various wave lengths for the photokinesis of Unionicola. *Jour. Cell. and Comp. Physiol.*, **9**: 453–67.

WELSH, J. H., 1933. Light intensity and the extent of activity of locomotor muscles as opposed to cilia. *Biol. Bull.*, **65**: 168–74.

WELSH, J. H., 1938. Diurnal rhythms. *Quart. Rev. Biol.*, **13**: 123–39.

WELSH, J. H., AND F. A. CHACE, JR., 1937. Eyes of deep sea crustaceans. I. Acanthephyridae. *Biol. Bull.*, **72**: 57–74.

WELSH, J. H., AND F. A. CHACE, JR., 1938. Eyes of deep-sea crustaceans. II. Sergestidae. *Ibid.*, **74**: 364–75.

WELSH, J. H., F. A. CHACE, JR., AND R. F. NUNNEMACHER, 1937. The diurnal migration of deep-water animals. *Ibid.*, **73**: 185–96.

WHITNEY, L. V., 1938. Transmission of solar energy and the scattering produced by the suspensoids in lake waters. *Trans. Wisconsin Acad.*, **31**: 201–21.

Contribution No. 206

Reprinted from Biological Bulletin, Vol. LXXVI, No. 2, 280–303, April, 1939
Printed in U. S. A.

THE REPRODUCTION OF LIMACINA RETROVERSA (FLEM.)

SIDNEY C. T. HSIAO

(From the Biological Laboratories, Harvard University, and the Woods Hole Oceanographic Institution,[1] Woods Hole, Massachusetts)

Introduction

The structure of the reproductive system of *Limacina retroversa* and the process of spermatogenesis of this species have been described in a previous paper (Hsiao, 1939). It was shown that very small animals are sexually undifferentiated. The gonads of sexually differentiated but small-sized individuals are protandric and many of them are often without female tissue, that is, " pure male," while those of the bigger animals are essentially hermaphroditic, showing different proportions of male and female tissues. Some individuals function as male, others as female and still others both as male and female at the same time. It is the purpose of this study to examine the relationship between size and sexual phases and the time of the occurrence of the latter so as to determine their sequence in the reproductive history of this form and to compare it with other mollusks whose sexual history is known.

Description of Material

The material was collected by the research vessel " Atlantis " during a series of cruises in the Gulf of Maine between June, 1933 and September, 1934. Specimens collected at the following periods were used:

Date	Designated as
December 2–11, 1933	December specimens
January 9–13, 1934	January specimens
March 21–28, 1934	March specimens
April 17–May 13, 1934	April specimens
May 21–June 2, 1934	May specimens
June 25–July 1, 1934	June specimens
September 17–24, 1934	September specimens

The specimens were caught by vertical hauls made with a 1.5-meter Heligoland larva net drawn from a level near the bottom up to the surface and fixed on board the ship in 2 per cent formalin in sea water.

---

[1] Contribution No. 206 from the Woods Hole Oceanographic Institution.

Limacina retroversa were later sorted out from the other species and specimens were selected from one to three stations from each cruise so as to make a series covering nearly the whole range of size. Each individual was measured with shell-opening facing the observer under a binocular microscope with a calibrated ocular micrometer. The diameter of the largest whorl of the spiral body of the animal, excluding the protruding margin of the shell-opening (*A–B* in Fig. 1), was measured and used to designate the size of the specimens studied.

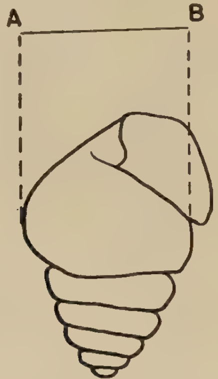


FIG. 1. Camera lucida drawing of the shell of *Limacina retroversa*. × 20. *A B:* maximum diameter of the shell used for comparison of size.

From a study of the size distribution of *Limacina retroversa* from 1933–34 and the movement of the water masses, Redfield (1939) has shown that at least two different populations entered the Gulf of Maine during the period of observation. The first group, called "population A," invaded the Gulf during December, 1933 and January, 1934, and later in the spring a second group, "population B," entered the basin during April and May from the same general direction. The positions of the hydrographic stations from which specimens used in this study were taken are shown in Fig. 2. In this map the solid circles with the abbreviations of the months beside them show the position and time of collection of the material from the population of *Limacina retroversa,* which has been identified as "population A" by Redfield. The positions of the stations providing the material fall within the region where large numbers of "population A" were found (as shown by Redfield's map), that is, in or near the center of density of this population in the different months. On the same map (Fig. 2) the open circles, with the abbreviations of the months in parentheses under them, indicate the stations in April and May from which specimens were selected which represent "population B." From these specimens the reproductive history of the species is worked out. The following table (Table I) shows the number of individuals used from each cruise grouped into size classes with a class interval of 0.3 mm.

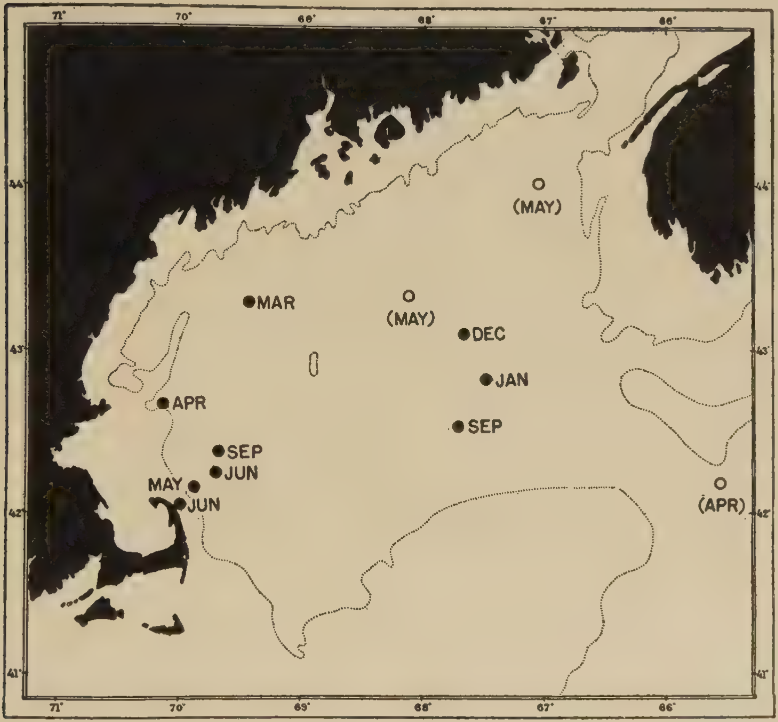


FIG. 2. Map of the Gulf of Maine showing the hydrographic stations from which samples of *Limacina retroversa* are selected for microscopic study.

●: stations for "population A."
○: stations for "population B."

The method employed in making serial sections of these specimens has been described in a previous paper. The following observations are based upon a comparative study of these serial sections.

Relation Between Size and Sex

The relation between size and sex in *Limacina retroversa* has been examined from two different angles: (1) The gonadal types and size, and (2) the relation between functional types and size.

Gonadal Types and Size

The following morphological types are seen among *Limacina.* (*a*) Sexually undifferentiated individuals all of which are small-sized; (*b*) "pure males" which are nearly completely male in constitution and are somewhat larger; and (*c*) hermaphrodites, which have various proportions of male and female tissues in the ovotestis and are generally of large size. The occurrence of the different morphological types of individuals in *Limacina retroversa,* in order of size, is shown in Table II.

Sexually Undifferentiated Individuals.—Of all the *Limacina retroversa* sectioned the largest individual which has a gonad still in a sexually undifferentiated condition measures 0.85 mm. in diameter. Individuals larger than this size all show definite gametogenesis. All specimens with a diameter less than 0.6 mm. are sexually undifferentiated. Hence, the process of sexual differentiation must commence during the period when the animal is between 0.6 mm. and 0.85 mm. in diameter. This is brought out more clearly when the percentage of sexually undifferentiated individuals is plotted against size as shown in Fig. 3.

TABLE I

Table showing the number of individuals from each period of collection which were used in this study. The individuals are separated according to size into groups with a class interval of 0.3 mm.

Month of cruise	Size groups in mm.								Total number obtained during month
	0 to 0.3 mm.	0.3 to 0.6 mm.	0.6 to 0.9 mm.	0.9 to 1.2 mm.	1.2 to 1.5 mm.	1.5 to 1.8 mm.	1.8 to 2.1 mm.	2.1 to 2.5 mm.	
Dec.	3	13	9	8					33
Jan.		13	12	4	3				32
Mar.		4	4	7	10	1			26
Apr.			5	9	5	6	1		26
May	4	11	7	6	3	6	2	1	40
June	4	3	6	2	6	5	2		28
Sept.	1	6	8	7	4	3			29

"Pure Males."—These are animals with gonads which contain little or no noticeable amount of ovarian tissue. They correspond to Coe's "true males" or Orton's "pure males." These individuals are confined to comparatively small-sized groups. Table II, column 8, shows the sudden appearance and the steady but more gradual decrease of "pure males" among animals arranged in the order of increasing size. Among larger animals this type of individual gives place to those which have

various proportions of feminine reproductive cells in the gonads. These are the hermaphrodites described in the next paragraph. On the average, about 22 per cent of the specimens less than 1.2 mm. in diameter belong to the " pure male " class. Many of these males are functional at the time of fixation as shown by the presence of mature spermatozoa in the gonoduct.

Animals with Various Proportions of Male and Female Tissues in the Gonads.—In addition to the sexually undifferentiated animals and the " pure males " a small number of animals less than 1 mm. in diameter may have gonads containing various proportions of male and female tissues at the same time. Of all the animals greater than 1.1 mm. in diameter no undifferentiated or " pure males " were found. They all contain spermary and ovarian tissues in the same gonad. Following the criteria described in a previous paper these hermaphroditic animals can be classified as hermaphroditic males or hermaphroditic females according to whether they have more than 50 per cent or less than 50 per cent of their gonadal tissues consisting of male reproductive elements. The proportion of these two kinds of individuals in the different size groups is

TABLE II

Proportion of different morphological types of *Limacina retroversa* separated into groups without regard to the time of collection. Animals smaller than 1.2 mm. in diameter are separated into 0.1 mm. classes, those larger than 1.2 mm., into 0.3 mm. classes.

1	2	3	4	5	6	7	8	9	10
Size in mm.	Total number	Undifferentiated	Pure male	>50% male	<50% male	Percentage undifferentiated	Percentage pure male	Percentage of >50% male	Percentage of <50% male
0.4	3	3	0	0	0	100	0	0	0
0.5	3	3	0	0	0	100	0	0	0
0.6	13	8	3	2	0	62	23	16	0
0.7	15	5	7	3	0	33	47	20	0
0.8	24	3	8	13	0	13	33	54	0
0.9	12	0	3	7	2	0	25	58	17
1.0	14	0	2	8	4	0	14	57	28
1.1	15	0	2	10	3	0	13	67	20
1.2 to 1.49	44	0	0	34	10	0	0	77	23
1.5 to 1.79	34	0	0	26	8	0	0	77	23
1.8 to 2.09	19	0	0	11	8	0	0	58	42
2.1 to 2.39	4	0	0	2	2	0	0	50	50
2.4 to 2.7	2	0	0	1	1	0	0	50	50

shown in Table II. Column 5 shows the number of individuals with more than 50 per cent of their gonadal tissue made up of masculine elements, excluding those which are already listed in column 4 as "pure males." It shows the number of hermaphroditic males only. The percentages of hermaphroditic males of this class are given in column 9. Column 10 shows the percentages of hermaphroditic females based on the numbers shown in column 6. A comparison of columns 9 and 10 will show that the minimal size of the hermaphroditic females is much greater than that of the hermaphroditic males. This occurrence of hermaphroditic males as well as "pure males" in smaller-sized animals when compared with the hermaphroditic females indicates that the male reproductive tissue is developed when the animals are smaller than is the case with the female cells of reproduction.

Owing to the small number of individuals in each size group among the larger animals the data in the lower half of Table II have been rearranged so that the class interval is three times as large as in the upper half. It will be seen that among animals smaller than 1.2 mm. the proportion of hermaphroditic males increases steadily while among those larger than this size the percentages decrease from 77 to 50. On the other hand, there is only a small proportion of hermaphroditic females among the smaller animals, but among the larger ones the percentage increases from 23 to 50. Approximately speaking, before the animals reach 1 mm. in diameter the proportion of males increases very rapidly, indicating an early proliferation of the male reproductive cells giving rise to the types of males whose gonads are predominantly masculine in appearance. After the animals grow to a size greater than 1.5 mm. in diameter the female reproductive cells overtake the male in development, thus bringing about a decrease in the proportion of hermaphroditic males after the 1.8 mm. size group and an increase in the predominantly feminine type. The decrease in the proportion of animals which are predominantly masculine continues until the animals are about 2 mm. in diameter, from which stage onward the two sexual types are equally numerous (Fig. 3).

The Relation between Functional Types and Size

In addition to the above morphological types, we can analyse our material into functional types. From the structure and the place of occurrence in the body of mature germ cells each *Limacina's* state of reproductive activity at the time of fixation can be deduced. Thus, when mature spermatozoa are seen in the gonoduct, or at the base of the penis, the individual is obviously functioning as a male and can be classified as an *active male*. When mature ova are found in the ovotestis the individual can be considered as a *mature female,* while the presence of ripe eggs in the gonoduct indicates that the individual is a *spawning female.* The simultaneous presence of mature spermatozoa in the gonoduct and ripe ova in or out of the gonad is an indication that the individual is a *functional hermaphrodite,* to use Coe's terminology. The occurrence of these functional types is shown in Table III.

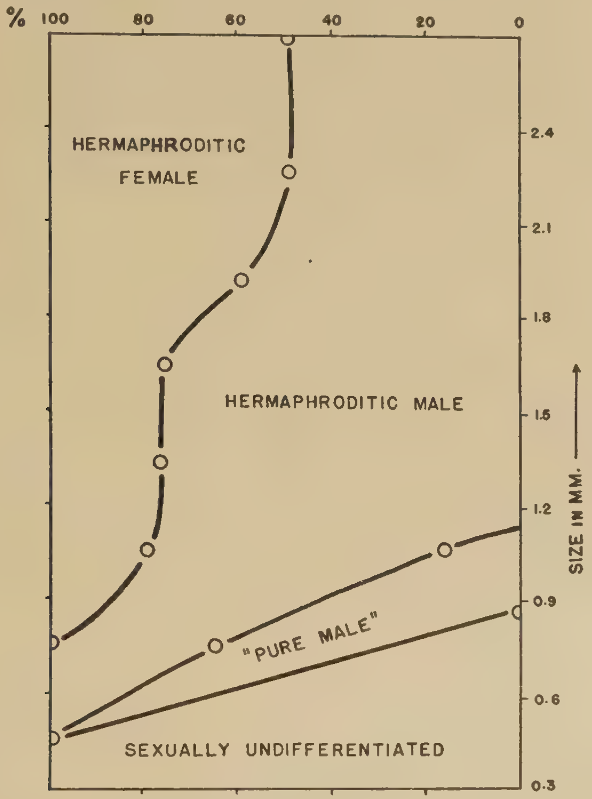


Fig. 3. Diagram showing the relation between size and various morphological types of gonads of *Limacina retroversa* (expressed in percentages of the total of each size group).

It has been observed that some individuals as small as 0.7 mm. in diameter may function as males. But the majority of specimens actively functioning as males only are between 1.2 mm. and 1.8 mm. in diameter (column 4). In larger-sized groups their place is taken by the females and individuals functioning both as male and female simultaneously.

The proportion of mature females with ripe eggs in the gonad, on the contrary, increases with the increase of size. The class with the largest number of mature females, as shown in Table III, is the 2.1 to 2.4 mm. group. The smallest *Limacina* with mature ova is more than 1 mm. in diameter. At the time of fixation many mature females were in the act of spawning, as evidenced by the presence of ripe ova at various points along the gonoduct. Roughly speaking, about half of the mature females in each size group were in the act of spawning when fixed.

The proportion of the third functional type, functional hermaphrodites, in each size group is shown in column 6 of Table III. The chief occurrence of this type of animal is among the larger-sized specimens. It will be seen from Table III that although both specimens of the 2.4–2.7 mm. size group are functional hermaphrodites, the number of individuals used is so small that no great importance can be attached to the deduced percentage of this type of animal. Until more large specimens are studied it seems better to leave this group out in our examination of the relation between the functional types and size. In the 2.1–2.4 mm. size group mature females and functional hermaphrodites are equally numerous.

TABLE III

Proportion of different functional types of *Limacina retroversa* expressed as percentage of each size group irrespective of the time of collection. Class interval: 0.3 mm.

1	2	3	4	5	6	7
Size groups (mm.)	Total number	Undifferentiated	Active male	Mature female	Functional hermaphrodite	Without signs of activity
		per cent	*per cent*	*per cent*	*per cent*	*per cent*
0.3–0.6.....	6	100	0	0	0	
0.6–0.9.....	52	30	17	0	0	53
0.9–1.2.....	41	0	39	15	5	41
1.2–1.5.....	44	0	48	9	14	29
1.5–1.8.....	43	0	47	18	21	14
1.8–2.1.....	19	0	5	42	10	43
2.1–2.4.....	4	0	0	50	50	0
2.4–2.7.....	2	0	0	0	100	0

When the gonads of these functional hermaphrodites are examined and classified in terms of the proportion of masculine and feminine tissue in them the following relationship is seen.

Type of gonad:	Percentage of specimens
With more than 75% male tissue..................	57%
With 50%–75% male tissue....................	33%
With 25%–50% male tissue.....................	10%
With less than 25% male tissue..................	0%

Most functional hermaphrodites have more than 75 per cent of the gonadal tissue made of male reproductive cells, one-third of them have a 50 per cent to 75 per cent male type of gonad, while no *Limacina* with less than 25 per cent male tissue in the gonad, that is, no very pronounced female type of individual, functions as hermaphrodite. Since the gonad of this species of pteropod changes from predominantly male to predominantly female type as the animals grow (see Fig. 3), this relation between the proportion of functional hermaphrodites and the amount of masculine tissue in the gonad can be interpreted to mean that animals possessing "more than 75 per cent male" type of gonad later have their female germ cells developed while the male phase of reproduction is still functioning, thus giving rise to a large proportion of hermaphrodites functioning as male and female at the same time. By the time the gonads change over to the predominantly feminine condition the male phase of sexual activity also disappears and hence few or no functional hermaphrodites are seen among individuals with a pronounced feminine type of gonad.

Figure 3 summarizes the facts about the relation of size to sexuality. Sexual differentiation commences during the time when the animals are between 0.6 and 0.9 mm. in diameter. The male germ cells proliferate in smaller-sized individuals giving rise to the "pure males" and hermaphroditic males before the animal reaches 1.2 mm. in diameter. The proportion of "pure males" decreases with increase in size. As the size increases further, the proportion of hermaphroditic males decreases, while that of the hermaphroditic females becomes greater and greater until the two sexual types are equal in number among animals greater than 2 mm. in diameter.

Functionally the situation is summarized in Fig. 4. The male phase starts among smaller *Limacina* than the functional female and hermaphroditic phases. The highest proportion of actively functioning males is found among animals 1.2 to 1.8 mm. in diameter. The large proportion of mature females and functional hermaphrodites occurs among larger animals replacing the male phase in those size groups. Females become mature after they have attained a diameter greater than 1 mm. It is probable that mature females and functional hermaphrodites are equally numerous among animals greater than 2 mm. in diameter. The percentage of each of these three functional types among the different size groups is shown in Fig. 4.

Seasonal Changes in the Reproductive Cycle

When the condition of the reproductive system of individuals collected at different times of the year is examined comparatively it is found that, as a general rule, in winter individuals are small protandric males and that later hermaphrodites and functional males and females appear. We shall first take up the morphological types of sexual individuals and the question of the proportion of these sexual types in different months, then the appearance of different sexual activities at various times of the year and lastly the question of the reversal of sex predominance. It has been shown by Redfield (1939) that " population A " can be clearly differentiated from " population B " from December up to May and after that time there is a good deal of mixing of populations with " population B " predominating over the descendants and remnants of " population A " and new recruits into the Gulf. In the following description data from December to May refer to " population A " and those after May, to the mixed populations.

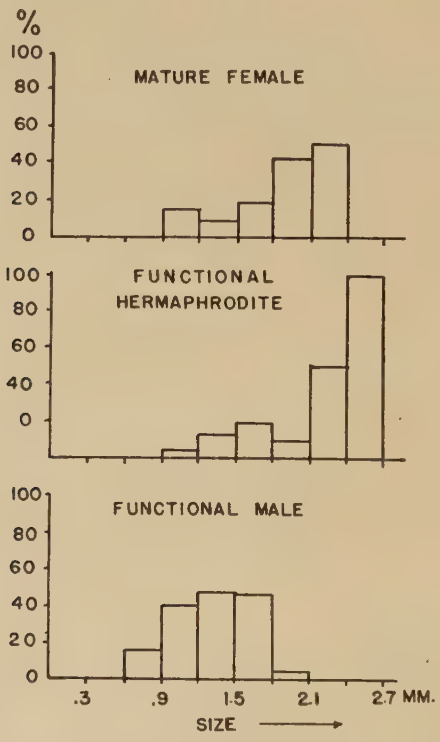


FIG. 4. Distribution of the three functional types of *Limacina retroversa* among various size groups. Functional males occur among smaller-sized animals than functional hermaphrodites and mature females.

Change in Gonad Structure

Young sexually undifferentiated individuals were found among the specimens taken in each month except March and April. Figure 5 shows the percentage of the individuals taken each month which are sexually indefinite. During the winter months of December and January "population A," which entered the Gulf then, contained 14–16 per cent of sexually undifferentiated animals. In March and April these animals drifted to the western portion of the Gulf and grew larger, as shown by Redfield, and there remained no sexually undifferentiated individuals. After May, a portion of the animals examined, 19–20 per cent, were again sexually indefinite. This coincides with the entrance into the Gulf of a new population in the east and the spawning of "population A" in the west portion of the basin. As far as "population A" is concerned, sexual differentiation is completed by the month of March and all the individuals of this population were either developing in the direction of males or hermaphrodites.

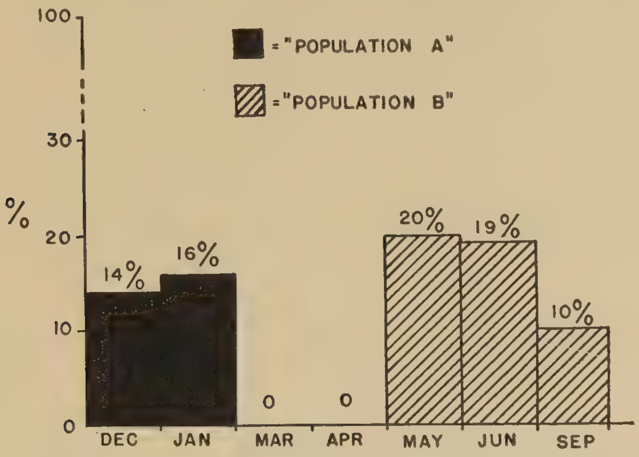


FIG. 5. Histogram showing the percentage of sexually undifferentiated individuals in each month. "Population A" solid black, "population B" shaded with straight lines. About 15 per cent of the material caught (in the winter) from "population A" and 20 per cent from "population B" are sexually undifferentiated. Absence of immature material in March and April indicates that members of "population A" are all differentiated by March.

Animals which were sexually differentiated have been divided into male or female type according to whether they had more or less than 50 per cent of their gonadal tissue made of male reproductive cells. The proportions of these male and female types among sexually differentiated *Limacina* collected each month are shown in Fig. 6. In this figure the material before May refers to "population A" and that after May to the mixed populations, with "population B" as the predominating constituent. It will be seen that in December and January nearly all the sexually differentiated *Limacina* were predominantly male. After these months the proportion of predominantly male individuals became reduced: in April they constituted only 40 per cent, while in May the two sexual types were equally numerous. After May the proportion of predominantly male animals became more numerous again among the mixed populations.

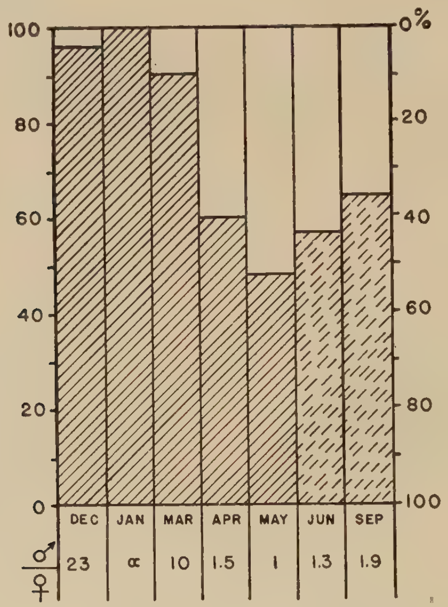


Fig. 6. Proportions of hermaphroditic males and hermaphroditic females among sexually differentiated *Limacina retroversa* in each month. Unshaded area represents hermaphroditic females, shaded areas hermaphroditic males. Area shaded with continuous lines refers to "population A," that with broken line, to "population B." ♂/♀ refers to the ratio of sex predominance in each month.

When the change in the percentage of the two sexual types among sexually differentiated *Limacina* from month to month as shown in Fig. 6 is calculated into ratios of sex predominance (the number of predominantly male individuals over those predominantly feminine) a change from a high value to unity is seen. These values are appended at the bottom of Fig. 6. It will be seen that in December and January this value is very high, but in May it is equal to one, while among the mixed populations the value is again in favor of the male type in the later part of the year.

In Fig. 7 are shown the proportions of " pure males," animals with little or no feminine tissue in the gonad, and " less than 25 per cent " male (very pronounced feminine) types among the sexually differentiated individuals in each month. About 45–55 per cent of sexually differentiated *Limacina* in December and January were " pure males," the rest being hermaphroditic males. In March the proportion of " pure males " was reduced greatly and from April onward this type of individual was not seen any more. On the other hand, pronounced feminine individuals with less than 25 per cent of the gonadal tissue made of male germ cells were not seen before May. It will also be noticed that the occurrence of this type of extreme female in the later part of the year has been always low in comparison to the other types.

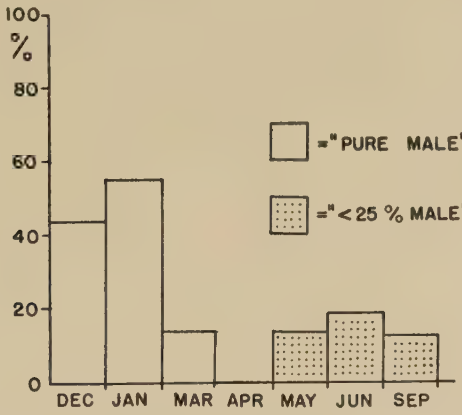


FIG. 7. Monthly appearance of " pure males " and hermaphroditic females with less than 25 per cent of their gonadal tissue consisting of male germ cells. Histograms before April refer to " population A " and those after April to " population B " with mixed populations. " Pure males " represented by unshaded areas; " less than 25 per cent male " type of hermaphroditic females represented by shaded areas.

Change in Reproductive Activity

The reproductive activities of *Limacina retroversa* show a parallelism with the morphological changes associated with the advance of time. During December and January when " pure " and hermaphroditic males constituted nearly all the groups of sexually differentiated individuals no hermaphroditic females with mature ova in the gonad were seen in the specimens examined, while spermatozoa, on the other hand, were evidenced as being liberated by the fact that mature male germ cells were found in different parts of the gonoduct. It is in March, however, that individuals with mature ova in their ovotestes began to appear. This type of individual continued to increase in proportion until May. In May animals had been collected and fixed during their spawning activity. Later in the year all the different types of functional individual were seen. The occurrence of these types of functional individual in the various months is shown in Table IV.

Table IV

Distribution of functional types of *Limacina retroversa*, expressed in percentages, in different months.

1	2	3	4	5	6
Month	Number studied	Active males	Mature females	Spawning females	Functional hermaphrodites
		per cent	*per cent*	*per cent*	*per cent*
Dec.	24	63	0	0	0
Jan.	26	58	0	0	0
Mar.	22	55	5	0	0
Apr.	25	32	20	0	8
May	23	17	43	30	26
June	21	19	38	19	19
Sept.	26	19	27	12	35

It will be seen from column 3 of this table that individuals ready to liberate spermatozoa are seen throughout the year, but that the proportion is higher in the earlier part of the year than in the later and that the reduction of the number of active males is accompanied by an increase in the number of individuals functioning as females (columns 4 and 5) and those acting as hermaphrodites (column 6) after April. A comparison of columns 4 and 5 will show that spawning is found after the mature females were observed in March. It has been found in the section on the relation between size and sexuality that about half of all the mature females examined were fixed during the act of spawning. From column 5 of Table IV it is seen that in May about three-quarters of the mature females were fixed in this stage, while in June the proportion of spawning females amounted to half of the matured ones, and in September, less than half. This indicates a higher spawning activity in May than in the other months. The fact that no spawning individuals were seen among the mature females in April does not exclude the possibility that egg-spawning took place in this month but that the individuals did not happen to be fixed with eggs in the gonoduct and selected for examination in this study. We may consider spawning to start between April and May and continue to the fall with May as the most important period for breeding.

From the above examination of the reproductive system of *Limacina* in terms of time it appears that among "population A," which entered the Gulf of Maine first, all the individuals were sexually differentiated by the beginning of March. In winter, a great majority, if not all, of them were "pure males." The number of such "pure males" decreased in March and they were not seen in April, giving place to individuals with a lesser degree of masculinity, to functional hermaphrodites and eventually to hermaphroditic females with very little masculine tissue in their gonads. The proportion of male tissue in comparison with the female in the gonad decreased as the animals grew. By April 40 per cent of the specimens collected had the feminine tissue so well developed as to warrant their being classified as hermaphroditic females. Animals with "less than 25 per cent male" gonads occurred after the "pure males" had disappeared from the collections. In May the two sexual types were equal in number. After May the bulk of the species in the Gulf was derived from the recently arrived "population B" which mixed with the descendants and remnants of "population A" and other new recruits. Among the mixed population sexually undifferentiated individuals were seen again and all the structural types were present.

The functional phases of reproduction are summarized in Fig. 8. More than half of the protandric males started to function in winter and the male phase continued into spring and summer as it became gradually replaced by the female and functional hermaphroditic phases of reproduction. Females began to attain maturation in March and the proportion of mature females increased rapidly in April and May. Spawning of ova commenced between April and May, being highest in the latter month. The largest proportion of functional individuals, including the male, female, and hermaphroditic types, is seen in May when half of them were spawners of eggs and the other half were males and hermaphrodites in function. These individuals were seen in the months from June to September also. It appears that May is the most important period for spawning though the reproductive activity was carried on into the autumn.

Change in Sex Predominance

A change in the value of the ratio of the sexes during growth is generally used as one of the indications of a change of sex. As the term "sex ratio" is not very appropriate for monoecious forms where both male and female reproductive tissues are present in the gonad, it seems better to speak of sex predominance and ratio between male and female predominance. The decrease in the value of this ratio from small to large-sized animals may be due, in general, to any one of the following causes: (*a*) Sexual dimorphism such that the males are habitually smaller than the females, (*b*) differential mortality, that is, more males than females die as the animals grow, and (*c*) sex reversal or an actual change in the condition of the reproductive system as the animals grow. There is no evidence from our material either to show that there

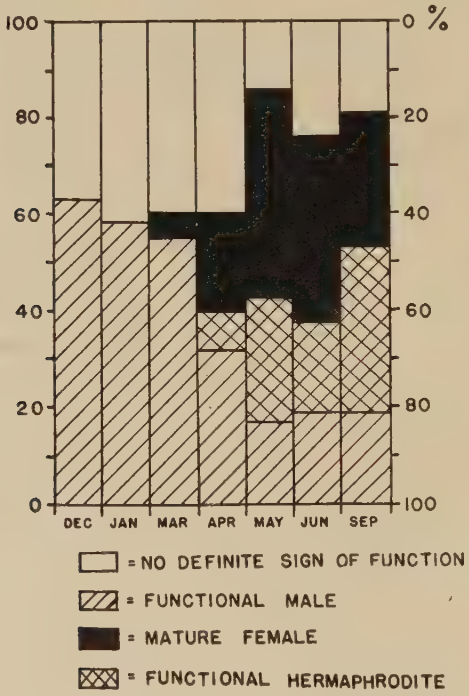


FIG. 8. Monthly distribution of the three functional types of *Limacina retroversa.*

is a sexual dimorphism or to indicate a differential mortality which may be interpreted as the cause of the appearance of a higher proportion of males among smaller-sized *Limacina* and a greater number of females among larger ones. The third alternative, that a change in the predominant sexuality takes place as the animals grow, however, has much evidence in its favor. In the first place, it has been shown above that there is a parallelism between the changes in the ratio of sex predominance with reference to size and that with reference to the advance of the season: male types dominate among smaller-sized *Limacina* and during the winter months, and this excess of males decreases as the animals become larger and also as the season advances, and eventually the two types become equal among still larger-sized specimens and at the height of the breeding season in May. This parallelism indicates a change in the sexuality, both in structure and function, of the individuals as they grow.

In the second place, it has already been shown in a previous paper that there is no clear line of demarcation between male and female among *Limacina,* but that hermaphroditic male and female merge into each other and that a continuous series can be made out. As the size of the animals increases, a greater and greater portion of the gonad appears to contain female tissue. "Pure males" are confined to small-sized animals and in the winter months. The continuous change in the proportion of male and female reproductive tissues in the gonad culminating in many functional hermaphrodites and females with less than 25 per cent of the tissue of their sex glands made of masculine elements argues in favor of a reversal of sex predominance in this species. Furthermore, there is no "pure female" among *Limacina:* all the hermaphroditic females are large and apparently derived from male types.

Thirdly, a comparison of the size distribution of the different sexual types in the various months also shows that there is a change in sex predominance. In Fig. 9 the proportions of (*a*) sexually undifferentiated young, (*b*) individuals which are predominantly masculine and (*c*) those which are predominantly feminine, have been indicated in the histograms prepared by Redfield showing the distribution of size among all the specimens taken during each cruise. It shows the earlier occurrence of protandric males and later appearance, in March and April, of female types. The appearance of the female type among larger size groups suggests that they are transformed from the protandric individuals rather than from the very small undifferentiated ones.

From these morphological male and female types of *Limacina* functional hermaphrodites have also been indicated in the same figure (Fig. 9). These functional hermaphrodites increase from a very small proportion in April to a maximum in May and then decline in June. This change in the relative proportion of this type of individual supports the idea mentioned above that protandric males develop ovarian tissue while they are still functioning as males and eventually become functional females.

Finally, if the modal class of each month's collection is taken as representative of the total catch, the phenomenon of change of sex predominance can be brought out when the different modal size groups are compared. Analysis of the size frequency distribution showed that

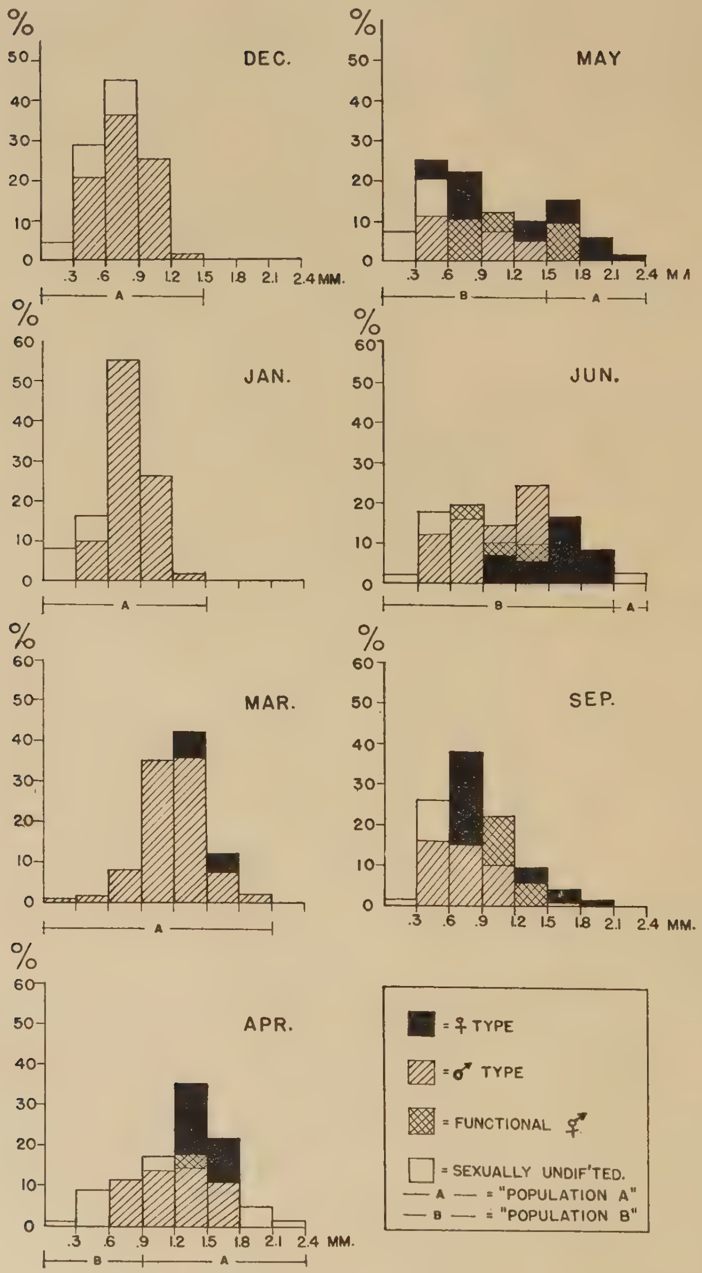


FIG. 9. Distribution of different types of *Limacina retroversa* among various size groups in each month. The proportion of each sexual type is added to the histogram showing size distribution prepared by Redfield (1939).

there is a single mode from December to April (Redfield, 1939). This modal class shifts from smaller to larger size during this period, showing a general growth of the members of the population. The sexual condition of the gonads of the modal class shows that not only growth, but sexual change has also taken place. In the modal class of the December material all the differentiated individuals are males and over 60 per cent of them have more than three-quarters of their gonadal tissues composed of male reproductive cells. Half of the males are ready to liberate spermatozoa. In January all the individuals of the modal class are predominantly male and 65 per cent of them are ready to discharge the product of their sex glands, thus showing an increase in the proportion of sexual differentiation with growth and an increase in the number of individuals capable of inseminating others. But it is in March that 11 per cent of the modal class are seen to have more female tissue in their gonads; the rest are still all predominantly male, half of which are ready to discharge or are discharging spermatozoa. The proportion of females increases to one-half of the modal class in April and some of the individuals begin to function both as male and female simultaneously. Of the two modal classes in May, the larger one shows, in the condition of the reproductive system, a continuation of the general changes of the previous months. For there is a further reduction of the male type and an increase of the functional hermaphrodites and actively functioning females. In this month, when the egg-laying individuals are added together, that is, spawning females plus functional hermaphrodites, they make up the whole of the modal class (see the right half of the histogram for May in Fig. 9). Thus if the modal class found by Redfield is taken as representative of the material collected, observations on the sexual condition of these groups give a consistent story of the change of sex predominance and function.

Relation between Sexual Phases and Distribution

When the sexual condition of populations A and B are compared several interesting differences are seen. The first characteristic of the sexual phases of " population B " in contrast to " population A " is that sexual differentiation seems to commence earlier with reference to size. In " population A " individuals as large as 0.85 mm. in diameter have been seen as undifferentiated sexually, while the largest undifferentiated individual of " population B " is only 0.6 mm. in diameter. In addition to the earlier differentiation of the gonads, a second difference is seen in the manner of differentiation between the two populations. Instead of the male elements in the gonads always taking the lead in development so as to bring about protandry, some individuals among " population B " have both types of sexual cells developed at nearly the same time in addition to protandry, so that proterogyny and hermaphroditism appear. In view of this type of development, small-sized mature hermaphroditic females and functional hermaphrodites may also be interpreted as derived directly from young undifferentiated individuals with the protandric stage omitted. In " population A " such a situation is not seen. The third point of difference is that the development of the female elements of the gonads of individuals in " population B " is also earlier. This can be seen when the minima of the size of the individuals which achieved maturation of ova in the two populations are compared. The minimal size of *Limacina* with mature ova is 0.8 mm. in diameter in April and 1 mm. in May among members of " population B," while among " population A " the minimal size of mature females is 1.3 mm. in April and 1.67 mm. in May. It is possible that these small mature females in " population B " did not pass through a protandric stage of noticeable length, though other specimens of the same population have a distinct young male phase preceding the female. In " population A " the smallest functional hermaphrodite is 1.5 mm. in diameter in April and 1.6 mm. in May, while during the same months functional hermaphrodites as small as 1.1 mm. in diameter are found among " population B."

In Fig. 9 the right portion of the May histogram which has been attributed to " population A " by Redfield is very similar to that of April in the distribution of sexual types. In both cases hermaphroditic females occupy the large size groups with functional hermaphrodites between them and the small-sized, predominantly male individuals. On the other hand, the left portion which represents " population B," has a size distribution comparable to those of the winter polygons but the sexual phases are quite different from them. Here the hermaphroditic females and functional hermaphrodites appear among protandric males in small size groups, which in the previous months only contain protandric and " pure " males.

All these differences in the sexual condition of the two populations seem to point convergingly to one underlying factor, namely, that during the warmer part of the year sexual differentiation takes place sooner than in the colder time and the sexual phases may be telescoped together when differentiation is speeded up in the summer. This is in line with the previous observations made on *Ostrea* by authors on both sides of the Atlantic (Coe, 1932, 1936; Needler, 1932; Orton, 1926; Spärck, 1925). However, this does not exclude the possibility that there is a difference in the origin of "populations A and B" which may account for some of the observed differences in sexual development.

COMPARISON OF THE REPRODUCTION OF LIMACINA RETROVERSA WITH OTHER MOLLUSKS

As the reproductive history of no other Opisthobranchiata has been described, it is not possible to compare the reproduction of *Limacina retroversa* with that of the members of the same genus or family or even order. Only in a general way can the sexual sequence of this form be compared with that found among other mollusks.

In the winter months *Limacina* which entered the Gulf of Maine are of small size and sexually undifferentiated. As they grow this initial phase is followed by protandry in which nearly all the individuals are predominantly male. The protandric phase is succeeded by a hermaphroditic phase during which the animals transform from a more masculine to a more feminine condition. In the final phase the individuals are predominantly female in structure and generally function as hermaphrodites, liberating both ova and spermatozoa, or as females only. This type of sexual transformation conforms in a general way with that found among gastropods. The sequence approximates most closely to that of the prosobranchiate gastropods such as *Valvata tricarinata* worked out by Furrow (1935) and *Patella vulgata* by Orton (1928). But the time required for the transformation of sex is different. Orton observed that the male *Patella* transformed into female at the age of one year, while Furrow found that in *Valvata* the different sexually functional phases followed each other very closely and the protandric phase was very short. However, in *Limacina retroversa* the change in sex predominance seems to take place during a period of two or three months. For instance, in one population which entered the Gulf of Maine in December and January, the protandric males were transformed into females from March to May. In the warmer part of the year this transformation required a shorter time for its completion.

SUMMARY

1. In the winter months sexual differentiation commences when the animals are between 0.6 and 0.85 mm. in diameter. In the summer sexual differentiation starts when the animals are smaller.

2. The early proliferation of the male reproductive cells leads to a protandric phase. The "pure males" give place to hermaphroditic males and later to hermaphroditic females as the size of the animals becomes greater than 1 mm. in diameter. After the specimens are 1.5

mm. in diameter the female reproductive cells overtake the male in development, bringing about a decrease in the proportion of hermaphroditic males and an increase of the opposite sexual type. This change continues until the two types are equal, when the animals are 2 mm. or more in diameter.

3. Functionally the male phase starts among smaller *Limacina* than do the functional female and hermaphroditic phases. The highest proportion of actively functioning males is found among animals 1.2 to 1.8 mm. in diameter. Among larger animals the functional hermaphroditic and functional female phases replace the male phase. Hermaphroditic females begin the functional phase after they are greater than 1 mm. in diameter.

4. Members of a population which entered the Gulf of Maine in the winter were all sexually differentiated by the beginning of March. Nearly all of these individuals developed into protandric males, about half of which were "pure males." The number of such "pure males" decreased in March and disappeared in April, being replaced by animals with greater predominance of feminine tissue in the gonads. By April about 40 per cent of the specimens were hermaphroditic females and in May the two sexual types were equal.

5. The male functional phase began in winter and continued into spring and summer. Hermaphroditic females matured in March and their proportion increased in April and May. Spawning of ova commenced by the end of April. The largest proportion of functional individuals of all types was seen in May.

6. Reasons are advanced for the belief that the change in sexual constitution of the populations is due to a reversal of sex predominance of the individuals.

7. The sequence of the sexual phases of *Limacina retroversa* agrees in a general way with those found for other members of the gastropod group of mollusks, particularly that of *Valvata.*

This study has been carried out under the helpful direction of Professor Redfield to whom the writer wishes to express his indebtedness.

BIBLIOGRAPHY

AMEMIYA, I., 1929. On the sex change in the Japanese common oyster, Ostrea gigas Thunberg. *Proc. Imper. Acad. Tokyo,* **5**: 284.

AWAITI, P. R., AND H. S. RAI, 1931. Ostrea cucullata (Bombay oyster). *Indian Zoöl. Mem.,* **3**: 1.

BOUCHON-BRANDELY, M., 1882. On the sexuality of the common oyster (O. edulis) and that of the Portuguese oyster (O. angulata). Artificial fecundation of the Portuguese oyster. *Bull. U. S. Fish. Com.,* **2**: 339.

Burkenroad, M. D., 1931. Sex in the Louisiana oyster, Ostrea virginica. *Science,* **74**: 71.

Coe, W. R., 1931. Sexual rhythm in the California oyster (Ostrea lurida). *Science,* **74**: 247.

Coe, W. R., 1932*a*. Sexual phases in the American oyster (Ostrea virginica). *Biol. Bull.,* **63**: 419.

Coe, W. R., 1932*b*. Development of the gonads and the sequence of the sexual phases in the California oyster (Ostrea lurida). *Bull. Scripps. Inst. Ocean. Tech. Ser.,* **3**: 119.

Coe, W. R., 1933. Sexual phases in Teredo. *Biol. Bull.,* **65**: 283.

Coe, W. R., 1934*a*. Alteration of sexuality in oysters. *Am. Nat.,* **68**: 236.

Coe, W. R., 1934*b*. Sexual rhythm in the pelecypod mollusk Teredo. *Science,* **80**: 192.

Coe, W. R., 1935*a*. Influence of external stimuli in changing the sexual phase in mollusks of the genus Crepidula. *Anat. Rec.,* Suppl., **64**: 80.

Coe, W. R., 1935*b*. Sequence of sexual phases in Teredo, Ostrea and Crepidula. *Anat. Rec.,* **64**: 81 (suppl.).

Coe, W. R., 1936*a*. Environment and sex in the oviparous oyster Ostrea virginica. *Biol. Bull.,* **71**: 353.

Coe, W. R., 1936*b*. Sequence of functional sexual phases in Teredo. *Biol. Bull.,* **71**: 122.

Coe, W. R., 1936*c*. Sexual phases in Crepidula. *Jour. Exper. Zoöl.,* **72**: 455.

Coe, W. R., 1936*d*. Sex ratio and sex changes in mollusks. Manifestation P. Pelseneer Bruxelle, p. 69.

Furrow, C. L., 1935. Development of the hermaphrodite genital organs of Valvata tricarinata. *Zeitschr. f. Zellforsch.,* **22**: 282.

Gemmill, J. F., 1896. On some cases of hermaphroditism in the limpet (Patella) with observations regarding the influence of nutrition on sex in the limpet. *Anat. Anzeig.,* **12**: 392.

Gemmill, J. F., 1900. Some negative evidence regarding the influence of nutrition on sex. *Communicat. Millport. Mar. Biol. Stat.,* **1**: 32.

Gould, H. N., 1917. Studies on sex in the hermaphrodite mollusk Crepidula plana. II. Influence of environment on sex. *Jour. Exper. Zoöl.,* **23**: 225. III. Transference of the male producing stimulus through sea-water. *Jour. Exper. Zoöl.,* **29**: 113.

Grave, B. H., and J. Smith, 1936. Sex inversion in Teredo navalis and its relation to sex ratios. *Biol. Bull.,* **70**: 332.

Gutsell, J. S., 1926. A hermaphroditic viviparous oyster on the Atlantic coast of North America. *Science,* **64**: 450.

Hsiao, Sidney C. T., 1939. The reproductive system and spermatogenesis of Limacina (Spiratella) retroversa (Flem.). *Biol. Bull.,* **76**: 7.

Loosanoff, V. L., 1937. Seasonal gonadal changes of adult clams, Venus mercenaria. *Biol. Bull.,* **72**: 406.

Needler, A. B., 1932*a*. Sex reversal in Ostrea virginica. *Con. Can. Biol. and Fish.,* **7**: 283.

Needler, A. B., 1932*b*. American Atlantic oysters change their sex. *Prog. Rept. Atl. Biol. Sta. and Fish. Exp. Sta.,* **5**: 3

Orton, J. H., 1909. On the occurrence of protandric hermaphroditism in the mollusc Crepidula fornicata. *Proc. Roy. Soc., Ser. B.* **81**: 468.

Orton, J. H., 1919. Sex-phenomena in the common limpet (Patella vulgata). Nature, **104**: 373.

Orton, J. H., 1922. The phenomena and conditions of sex-change in the oyster (O. edulis) and Crepidula. *Nature,* **110**: 212.

Orton, J. H., 1926. Observations and experiments on sex-change in the European oyster (O. edulis). *Jour. Mar. Biol. Ass'n,* **14**: 967.

Orton, J. H., 1928. Observations on Patella vulgata. *Jour. Mar. Biol. Ass'n,* **15**: 851.

Orton, J. H., 1931. Observations and experiments on sex-change in the European oyster (O. edulis). *Jour. Mar. Biol. Ass'n,* **17**: 315.

Pelseneer, P., 1894. Hermaphroditism in Mollusca. *Quart. Jour. Micr. Soc.,* **37**: 19.

Pelseneer, P., 1926. La proportion relative de sexes chez les animaux et particulièrement chez les mollusques. *Mem. Acad. Roy. Belg. Sci.,* **8**: 11.

Redfield, Alfred C., 1939. The history of a population of Limacina retroversa during its drift across the Gulf of Maine. *Biol. Bull.,* **76**: 26.

Spärck, R., 1925. Studies on the biology of the oyster. *Rept. Dan. Biol. Sta.,* **30**: 1.

Younge, C. M., 1926. Protandry in Teredo norvegica. *Quart. Jour. Micr. Soc.,* **70**: 391.

Contribution No. 207

Reprinted from BIOLOGICAL BULLETIN, Vol. LXXVII, No. 2, 200–215, Oct., 1939
Printed in U. S. A.

THE REACTIONS OF THE PLANKTONIC COPEPOD, CENTROPAGES TYPICUS, TO LIGHT AND GRAVITY[1]

W. H. JOHNSON AND J. E. G. RAYMONT

(*From the Department of Physiology, McGill University, the Biological Laboratories, Harvard University, and the Woods Hole Oceanographic Institution*)

INTRODUCTION

Field investigations on the vertical distribution of the plankton carried out by many different workers in recent years have established the occurrence of a diurnal vertical migration for most species of the zoöplankton. Since most investigators agree in considering light as an important controlling factor, it seemed desirable, following the work of Esterly, Spooner, Clarke and others, to attempt to study the light responses of a single planktonic species under controlled laboratory conditions.

Centropages typicus is a neritic copepod, extremely abundant off Woods Hole at certain times of the year. Clarke (1933) states that the adults show a diurnal vertical migration correlated with changes in the submarine illumination. A few preliminary observations in the laboratory showed us that the adult females are very definitely affected by light. It was therefore decided to conduct experiments on the phototropic and geotropic responses of these animals. Our choice was fortunate in that it was possible to obtain the copepods quickly and easily off Woods Hole, and to keep them at a conveniently low temperature in the laboratory to ensure their healthy existence for at least a few days.

PHOTOTROPISM: EXPERIMENTS WITH TUBES HORIZONTAL

In order to separate the phototropic from possible geotropic responses, it seemed advisable to test first the reactions of the copepods to light in a horizontal direction.

Methods

The experimental animals were obtained in Vineyard Sound by towing a scrim plankton net horizontally near the surface for about fifteen minutes. The animals, collected in the glass jar attached to the net, were poured into 3 liters of sea water and transported immediately to the laboratory. The adult female *Centropages typicus* were selected in diffuse daylight using a wide-mouthed pipette and a binocular microscope. Usually 20 healthy appearing copepods were placed in each of two glass tubes (13 × $2\frac{1}{2}''$), each of which was sealed at one end with a glass plate. The open ends of the tubes were then sealed with similar glass plates, and the tubes arranged in constant temperature tanks maintained at 12° C. in the darkroom.

---

[1] Contribution No. 207 from the Woods Hole Oceanographic Institution.

The two experimental tubes could be separated from each other by a distance of 21 feet. It was thus possible to obtain a wide range of light intensities for any one source, by varying the distance between the light source and the tubes. The intensities of the various inside frosted bulbs employed were as follows:[2]

Wattage	*Approximate Intensity at 1 foot*
15	13.5 foot-candles
25	25.0 "
40	43.0 "
60	75.0 "
100	150.0 "

It should be borne in mind that all the light intensities mentioned in the text are only approximate figures.

The lowest intensities used were obtained by means of neutral filters in the form of opal discs and white paper, the percentage absorptions of which were obtained by means of a photoelectric cell. Since several filters were used together at the very lowest intensities, corrections were made for diffusion and back-scattering.

Each experimental tube was marked off into quarter-lengths, and the distribution of the animals at any time, under any one condition of light, was expressed as the numbers in each section. At the very low light intensities, counting of the copepods was facilitated by lighting the tubes from behind for a moment with a weak red lamp. Preliminary tests made with this lamp showed that it had no effect on the distribution of the animals.[3]

In all the experiments, unless otherwise noted, the distribution of the animals was observed at the end of each time interval shown in the tables. After each observation, the tubes were changed, end for end, by turning them slowly in a horizontal plane. This procedure forced the animals to orientate afresh, and to redistribute themselves according to the tropistic responses actually in operation during that time interval. Enough time was allowed for the animals to establish their new distribution before a second record was taken, so that their final position was unaffected by the configuration of the previous time interval.

---

[2] On the advice of Mr. Eddie Kline, electrical engineer of the Canadian Laco Lamp Co., these can be considered as accurate only within 20 per cent, due to voltage fluctuation.

[3] Dr. Horton of the Department of Physics, McGill University, kindly made a spectroscopic photograph of the light emitted and found that the transmission begins at 6402 Å, and continues beyond 8600 Å.

TABLE I

Experiment commenced at 4:00 P.M., August 19.
Tubes *A* and *B* set at distance of 5 ft. and 1 ft. respectively, from source.
At 12:00 noon, August 20, tube *A* moved to 10 ft.
At 4:00 P.M., August 20, tube *A* moved to 20 ft.
Tube *B* was kept at 1 ft. throughout.
Source: 60-watt lamp.

Time	Distance	Intensity	(Positive) * I	II	III	(Negative) IV
Aug. 19 4:10 P.M.	5 ft.	3.0 f.c.	20	–	–	–
	1 ft.	75.0 f.c.	20	–	–	–
4:40 P.M.	5 ft.		20	–	–	–
	1 ft.		20	–	–	–
6:45 P.M.	5 ft.		16 and 4	–	–	–
	1 ft.		20	–	–	–
9:15 P.M.	5 ft.		10 and 6	–	2	3
	1 ft.		10 and 3	3	–	1
9:30 P.M.	5 ft.		8 and 6	–	2	2
	1 ft.		3 and 7	3	3	2
Aug. 20 11:30 P.M.	5 ft.		10 and 3	1	4	3
	1 ft.		4 and 8	3	1	1
2:30 P.M.	10 ft.	0.75 f.c.	8 and 3	–	3	3
	1 ft.	75.0 f.c.	5 and 9	3	1	1
4:00 P.M.	10 ft.		8 and 4	4	4	–
	1 ft.		3 and 7	4	1	1
4:45 P.M.	20 ft.	0.19 f.c.	9 and 6	–	3	–
	1 ft.	75.0 f.c.	5 and 10	3	2	1
8:00 P.M.	20 ft.		6 and 9	–	2	2
	1 ft.		3 and 9	4	1	2

* Two numbers are sometimes given under Section I (e.g. 16 and 4). This distinguishes those copepods right at the positive end (16), from those still in this section but apparently less strongly attracted.

Observations

A series of tests (Table I) was first carried out in order to determine:

(1) The normal responses of the copepods to various light intensities within limits found in nature.
(2) The effect of continued exposure to constant light intensities over the range studied.

The results obtained (Table I) showed that the copepods were positive to all illuminations, and remained largely so after exposure.

A number of experiments was then carried out to determine the range of light intensities to which the copepods were sensitive, and to investigate the possibility of the existence of critical light intensities at which the phototropic sign might become reversed.

The copepods were found to be positive to low light intensities, the lowest to which they were attracted being *ca.* 0.005 f.c. (Table II).

TABLE II

Responses to low light intensities. Distance of experimental tube from source: 20 ft. throughout.*

Intensity	Time	(Positive) I	II	III	(Negative) IV
0.06 f.c.	Aug. 20 9:30 P.M.	5 and 4	–	2	3
" "	Aug. 21 8:30 A.M.	4 and 6	1	2	1
0.015 "	10:45 A.M.	0 and 12	–	3	1
" "	12:00 Noon	2 and 12	1	2	3
" "	3:30 P.M.	4 and 5	1	4	–
0.008 "	Aug. 24 12:40 P.M.	14	1	3	2(New animals)
" "	2:00 P.M.	1 and 10	2	2	3
" "	3:00 P.M.	3 and 9	1	3	3
0.006 "	3:30 P.M.	11	2	1	3
" "	4:50 P.M.	6	5	–	7
" "	7:00 P.M.	11	2	2	1
" "	8:00 P.M.	10	–	2	7
" "	10:50 P.M.	13	–	4	1
" "	Aug. 25 8:30 A.M.	15	1	–	–
" "	9:30 A.M.	14	–	2	1
0.005 "	Aug. 26 12:30 P.M.	9	5	4	1
" "	1:55 P.M.	10	4	3	–
" "	2:25 P.M.	3	7	6	3
0.003 "	Aug. 28 2:30 P.M.	3	4	7	6(New animals)
" "	4:45 P.M.	9	4	4	3
" "	Aug. 29 9:40 A.M.	11	6	2	–
" "	11:50 A.M.	4	6	3	6
" "	6:45 P.M.	8	3	3	3

* Each time the light intensity was changed, it was done immediately following the preceding observation.

On continued exposure to the much higher light intensities of 150 and 600 f.c. (Table III), the majority of animals on the whole exhibited a positive phototropism, although at times there were more animals in the darker half of the tube and some of the animals apparently became negative on prolonged exposure.

It seemed desirable to determine whether the copepods would be repelled by the still higher light intensity (11,380 f.c.) approximating to that of bright sunlight. As a check on the results, other copepods which had been collected at the same time were subjected to a much lower intensity of 4 f.c. The results (Table IV) show that, at least after a short exposure to this very high intensity, half of the animals became negatively phototropic, while the others remained positive.

TABLE III

Responses to high light intensities
Source: 100-watt lamp. Intensity at ½ ft. : 600 f.c.
Intensity at 1 ft. : 150 f.c.

Time	Distance	(Positive) I	II	III	(Negative) IV
Aug. 30 5:00 P.M.	½ ft.	15	–	–	3
	1 ft.	14	–	2	3
5:30 P.M.	½ ft.	13	1	1	3
	1 ft.	13	–	1	6
6:45 P.M.	½ ft.	14	1	2	1
	1 ft.	10	1	–	8
9:00 P.M.	½ ft.	14	–	1	2
	1 ft.	14	1	2	3
10:15 P.M.	½ ft.	14	2	2	–
	1 ft.	10	–	1	8
Aug. 31 9:10 A.M.	½ ft.	5	1	2	10
	1 ft.	12	3	3	2
10:20 A.M.	½ ft.	8	1	3	7
	1 ft.	10	–	2	8
11:15 A.M.	½ ft.	11	2	1	4
	1 ft.	9	–	2	8
12:15 P.M.	½ ft.	9	1	1	8
	1 ft.	10	2	3	6
1:20 P.M.	½ ft.	12	2	–	4
	1 ft.	12	2	2	4
4:00 P.M.	½ ft.	12	2	–	4
	1 ft.	8	2	2	8
5:00 P.M.	½ ft.	12	1	3	3
	1 ft.	11	2	–	7

It was rarely that all the animals displayed an invariable reaction (either positive or negative) to any one condition of light. It was possible then that some of the animals were negatively phototropic even though the majority were positive; or again, perhaps some were indifferent. To gain evidence on these points, observations were made on individuals, one being sealed within a tube. At first, observations were made for the most part once every hour, using three widely separated intensities: 3.0, 150, and 600 f.c.

At the lowest intensity (3.0 f.c.), an individual remained photopositive for four hours, but appeared to become indifferent after exposure overnight. A second individual was indifferent from the first, and remained so for 15 hours. This behaviour was not modified if the individual was left in darkness, and then exposed to the light.

TABLE IV

Source: 1000-watt lamp. Tube at 4½ inches from source.
Control tube at 20 feet.
Ice added to aquarium to offset intense heat from source.

Time	Intensity	(Positive) I	II	III	(Negative) IV
11:40 A.M.	11,380 f.c.	10	–	2	6
	4 f.c.	8	4	1	6
11:55 A.M.	11,380 f.c.	12	–	–	6
	4 f.c.	11	2	–	5
12:05 P.M.	11,380 f.c.	8	1	–	9
12:20 P.M.	11,380 f.c.	10	–	4	6
	4 f.c.	13	–	2	3
1:20 P.M.	11,380 f.c.	8	1	2	10
	4 f.c.	11	2	2	3
1:35 P.M.	11,380 f.c.	9	1	3	8
1:45 P.M.	11,380 f.c.	8	1	3	8
	4 f.c.	15	2	2	–
2:00 P.M.	11,380 f.c.	9	–	–	9
2:10 P.M.	11,380 f.c.	10	1	1	7
	4 f.c.	14	2	1	1
2:25 P.M.	11,380 f.c.	11	1	–	7
2:40 P.M.	11,380 f.c.	8	1	–	11
	4 f.c.	14	2	1	1

The responses of two individuals at an intensity of 150 f.c., and of two others at 600 f.c. were such that one individual at each intensity remained positive for 24 hours, while the other individuals were positive for the first 5 hours but apparently became indifferent after exposure overnight.

More extensive experiments on individuals were carried out, making observations every ten minutes, so long as it was possible to do so, over a long period of time, and at a wide range of intensities (600, 150, 75, 67, 33, 13.5, 2.4, 0.87, 0.03, 0.006, and 0.002 f.c.). Of four individuals (*A*, *B*, *X*, and *Y*), specimens *B* and *Y* were strongly and constantly photopositive to all the above intensities; indeed, specimen *B* was never recorded outside Section I. Individual *A* was in the main attracted although less so at intensities above 75 f.c. Individual *X*, although less consistent, was generally attracted by the light, but occasionally at both high and low intensities it was found at the negative end of the tube, even from the beginning of the experiment.

Having studied the effects of continued exposure to different intensities, it was decided to determine the effect of changing light intensity—a condition which is more like that which occurs in nature. The changes in intensity were obtained by varying the position of the source relative to the two experimental tubes. Thus the quality of the light remained unchanged, and two experiments could be carried on at once.

Successive experiments were carried out by moving the source first 1 foot, then 2, 5, 10, and finally 20 feet every ten minutes (owing to difficulties in counting, 15-minute intervals were sometimes unavoidable). The intensities ranged from 11,380 to 4 f.c. Before the experiments were commenced, the tube at the maximum intensity was left exposed to light until a considerable percentage of the animals exhibited repulsion.

Regarding the one-foot changes: On increasing the intensity from 4 to 11,380 f.c., the animals remained continually attracted showing always at least 80 per cent in the positive half of the tube. However, after continued exposure for one hour at the highest intensity, only 40 per cent were still attracted. In the opposite tube, 55 per cent of the copepods were repelled at the beginning when the intensity was 11,380 f.c., and it was necessary to decrease the intensity to 64 f.c. before 80 per cent of the animals were attracted.

Considering the results of the 2 ft. changes, it was found that essentially similar conclusions could be reached. In the increasing intensity experiment, actually 100 per cent of the animals exhibited constant positive phototropism. Decreasing the intensity resulted in progressive attraction down to 16 f.c., when about 80 per cent of the animals were in Sections I and II. Further decreases caused little change.

The 5, 10 and 20-foot changes may be considered together. Regarding the increasing intensities, it is striking that none of the changes had any effect on altering the original distribution of the animals. The numbers of animals in each half of each tube remained almost perfectly constant with the ten-minute intervals allowed, and it was only after prolonged exposure (45 to 60 minutes) at 11,380 f.c. that repulsion was brought about. Of the decreasing intensity experiments, in the 5-ft. changes progressive attraction resulted in 80 per cent of the animals being positive at an intensity of 7 f.c. Progressive attraction also resulted in the other experiments, with 70 per cent of the animals being attracted in the 10-ft. changes at the minimum intensity of 4 f.c. (After one hour at 4 f.c., 80 per cent were positive.)

All these experiments on different magnitudes of decrease, each occurring with 10-minute intervals, would seem to indicate that the greater the magnitude of change, the lower the intensity at which a large number of the copepods became positively phototropic. This statement may be misinterpreted unless it be remembered that undoubtedly 80 per cent, or more, of the copepods would have migrated to the positive half of the tube at much higher intensities had more time been allowed before the next change was made. (There would thus appear to be a "time-lag" effect.)

The above experiments show the effects of different magnitudes of increase and decrease with a constant time interval of 10 minutes. The percentage relationship between any one intensity and that which immediately preceded it is not by any means constant during any one succession of changes. Thus experiments were next conducted similar to the foregoing, except that there was a constant percentage increase or decrease throughout each series of changes. The actual rates of change used were such as may occur in nature. (The values chosen were the maximal changes observed by Clarke (1933) at one station in the Gulf of Maine.)

Increases and decreases of 10 per cent per hour were first tried, through a range of high intensities (11,380 to 2,840 f.c.), and then through a low intensity range (9.5 to 6.2 f.c.). Considering first the decreasing intensities, through the high range there was progressive attraction, while through the low range there was practically no alteration in the distribution. As regards the increasing intensities experiment, there was little observable change, but, if anything, a rather larger percentage of animals was attracted with time. The same result was obtained with the low intensity range. Decreases and increases of 20 per cent per hour, through both high and low intensity ranges, gave similar results.

PHOTOTROPISM AND GEOTROPISM: EXPERIMENTS WITH TUBES VERTICAL

Parker, Dice, Esterly, Clarke and others have demonstrated that geotropism is frequently an important factor in the vertical migration of plankton. It seemed desirable, therefore, to carry out experiments using vertical tubes to ascertain whether the light responses would be different, and to test for the occurrence of a true geotropic reaction.

Methods

The aquaria were replaced by two large bell-jars held upright by specially constructed wooden stands. The same experimental tubes were used, but they stood vertically in all the following experiments. A lamp was suspended over each tube, and, by means of a pulley system, the distance between the lamp and the tube could be quickly altered. The maximum distance thus obtainable was 4½ feet. Whenever it was desired to illuminate the animals from below, the tubes were simply placed upright on an iron tripod, and the lamp placed underneath.

Observations

It was decided to find the effects of various rates of change of light intensity, and to compare the results with those obtained in the horizontal experiments. Unfortunately the 1,000-watt lamp burned out and as it was impossible to replace it in the short time remaining, it was necessary to confine the indoor experiments to the lower light intensities (0.67 to 240 f.c.). A wide variety of rates of change was used: 25 per cent per hour, and 25, 50, 100, 300, and 700 per cent per half-hour.

Considering the experiments on increasing light intensities the following conclusions were reached. Within the range of intensities used, it seemed that, in general, increasing the light at a variety of rates does not bring about repulsion. One experiment, however, using 25 per cent increases per half-hour, through a range from 7.4 to 19.1 f.c. did cause repulsion:—70 per cent of the copepods were attracted initially, but as the intensity increased, fewer remained positive until only 16 per cent were attracted at 19.1 f.c. A large number of other experiments, however, at intensities near 7.4 to 19.1 f.c. (also at higher and lower ranges, and at rates from 10 per cent to several hundred per cent) was carried out, and in no other case was this repulsion observed. In the great majority of cases the distribution remained almost constant. It may be then, that this single case of repulsion does not demonstrate the normal behaviour of these animals, at least under laboratory conditions.

In the experiments on decreasing light intensities, with the exception of a single experiment, decrease in intensity at all rates, and through all the ranges of intensity employed, resulted in more and more of the animals swimming to the top of the tube as the light diminished.

This progressive attraction was sometimes very great. For example, in two experiments only 25 per cent of the copepods were positive at the beginning, and nearly 90 per cent at the end. The exceptional experiment was the only one employing so low a rate of decrease as 10 per cent. It is possible that such changes are too slow to be perceptible to the animals (below threshold).

It was thought desirable to determine the effect of increasing light intensity, using direct sunlight, so that a very high intensity range would be available. The experiment was conducted in the open behind the Oceanographic Institution. An inverted bell-jar was used as in the darkroom, with the experimental tube placed inside it, standing vertically. Since it was here impossible to circulate cooled water through the bell-jar, it was simply refilled with cold sea water whenever the temperature rose. The stand holding the bell-jar was completely covered with black tar-paper. A small aperture cut in the top allowed a beam of sunlight to fall on the top of the experimental tube. On one side of the stand, the tar-paper formed a moveable flap which could be lifted, and the necessary counts made. Four opal diffusing discs were placed over the aperture to reduce the light; these were removed at intervals. In the first experiment, they were removed one at a time, in the second two at a time, and in the last experiment all four were removed together. Each disc alone transmits 25 per cent of the light falling upon it. The beam of sunlight was directed on to the aperture above the tube by means of a simple plane mirror which could be turned as the sun changed its elevation. The light intensity was measured by means of a Weston Photronic Cell.

TABLE V

Reactions to direct sunlight

Time	No. of Opals	Relative Sunlight	Approximate Int. in Tube (f.c.)	(Top) I	II	III	(Bottom) IV
		per cent					
12 Noon	4	100	1,080				
12:30 P.M.	4	100	1,080	11	1	4	3
1:00 P.M.	3	98	1,400	11	1	3	3
1:30 P.M.	2	93.6	2,000	12	1	1	4
2:00 P.M.	1	88	2,640	19	–	–	1
2:30 P.M.	0	79	9,470	11	2	1	5
3:00 P.M.	0	73	8,760	11	–	1	5
3:30 P.M.	4	59	636	12	–	3	3
4:00 P.M.	2	43.6	935	5	2	6	4
4:45 P.M.	0	27	3,240	7	1	3	7

The results of the experiment (Table V) show that when the light had increased from about 1,000 to about 9,000 f.c. over a period of two hours, the animals were at all times strongly photopositive. However, increases starting at lower intensities resulted in a majority of the animals in the lower half of each tube. Is there also a negative geotropism which becomes stronger with increase in light intensity? Certainly the results indicate that mere rate and direction of change of light alone cannot account completely for the movements of *Centropages typicus*.

Thus experiments were next carried out in order to test the possibility that the copepods might react to gravity, and that the above results were only partially due to phototropic responses.

The experimental tubes were placed vertically in the bell-jars in the normal way. The animals were then left in darkness, and counts made later with the red lamp. For example, the tubes were left for 1½ hours in darkness and subsequent counts gave the following results (Tubes *A* and *B* were treated identically to furnish checks on each other):

	(Top) I	II	III	(Bottom) IV
Tube *A*	14	4	1	–
Tube *B*	6	4	–	8

The tubes were then reversed vertically end for end. After one-half hour the following results were obtained:

	(Top) I	II	III	(Bottom) IV
Tube *A*	12	5	3	–
Tube *B*	12	3	–	3

The tubes were again reversed. After one-half hour the following results were obtained:

	(Top) I	II	III	(Bottom) IV
Tube *A*	11	3	1	2
Tube *B*	15	1	–	3

The above results clearly show that the animals are on the whole negatively geotropic in darkness. Careful observation showed that the animals sink rapidly if they cease swimming. Hence actual effort was necessary for them to remain at the tops of the tubes, and the geotropism must then be quite strong.

The relation between geotropism and phototropism was then tested by taking the above animals from darkness and illuminating them from below, with the following results:

	(Top) I	II	III	(Bottom) IV
Tube *A* (15-watt lamp below)	7	4	3	4
Tube *B* (100-watt lamp below)	–	1	–	19

The results would indicate that negative geotropism is stronger than positive phototropism when the light is weak, while positive phototropism is overwhelmingly strong when the intensity is high.

Tube *B* was returned to darkness and a count 15 minutes later showed that the majority of animals were in Section I.

These results verified the negative geotropism. A 60-watt lamp was then placed below the tubes and the following results obtained:

	(Top) I	II	III	(Bottom) IV
Tube *B* (60-watt lamp below the tube)......	1	–	–	19

Both tubes were again returned to darkness and a count 45 minutes later again showed a large majority exhibiting negative geotropism. A 25-watt lamp was then placed below the tubes:

	(Top) I	II	III	(Bottom) IV
Tube *B* (25-watt lamp below the tube)......	4	1	3	9

The experiment was repeated. The animals again showed negative geotropism in darkness. With a 25-watt lamp below the tubes the results were as follows:

	(Top) I	II	III	(Bottom) IV
Tube *B* (25-watt lamp below the tube)......	4	1	–	12

Finally it was decided to determine the effect of replacing a low light intensity by a high one, when the geotropism and phototropism were in opposition. It has been shown that after exhibiting negative geotropism in darkness, on exposure to a 25-watt bulb from below the distribution was:

	(Top) I	II	III	(Bottom) IV
Tube *B* (25-watt lamp below)..............	4	1	–	12

This lamp was then replaced by a 100-watt lamp. A count after 15 minutes showed:

	(Top) I	II	III	(Bottom) IV
Tube *B* (100-watt lamp below).............	–	–	–	17

All the above experiments definitely establish that the adult female *Centropages* is primarily negatively geotropic and positively phototropic. When the two are acting in opposition, the positive phototropism becomes progressively stronger as the light intensity increases.

Discussion

It is still a controversial matter how far laboratory experiments of the type conducted are applicable to conditions in nature. Throughout all the experiments, however, it was our aim to avoid "shock" conditions, and the use of surface tow-nettings avoided large changes in light intensity during the collections.

It would seem from the experiments with artificial light, that adult female *Centropages typicus* should be right at the surface during most of the day, since they are strongly positively phototropic to a very wide range of light intensities, and it does not seem that continual decreases are always necessary to cause a majority to remain positive, such as was found to be the case with *Acartia clausi* (Johnson, 1938). However, repulsion does occur to some extent on prolonged exposure to very high intensities, and also in the experiments using direct sunlight (Table V) when the illumination increased through such ranges of low intensities as may occur in the early morning. Hence, after considerable exposure to strong sunlight (about midday in summer) and possibly also when the light is increasing in the early morning, *Centropages* might be expected to be a little lower in the water.

G. L. Clarke (1933) however, found that these copepods have a maximum of about 13 m. during most of the day in the Gulf of Maine. Some hauls made in August, 1935, near Woods Hole, were examined and these in general confirmed this finding, although there were cases when the majority were at the surface. (Clarke also did find, for two stations, the majority at the surface.)

In considering this difference it must be remembered that there are other factors acting in nature. Thus, especially at the surface, turbulence may carry the copepods to somewhat lower depths. Further, the possibility of muscular fatigue must not be overlooked. As has been mentioned, *Centropages* will sink rapidly as soon as it ceases swimming, and thus some will tend to sink below the surface, though positively phototropic. This probably accounts for the observation, that, although using the same intensities, a considerably larger percentage of animals is found in the negative half of the tube in the vertical experiments than in the horizontal ones. It should also be noticed that Clarke did find a secondary maximum of *Centropages* at the surface.

The rise to the surface at night, observed by Clarke and others, is explainable since *Centropages* is always very strongly attracted when the light intensity is diminished. The negative geotropism, evident at least during and just after exposure to darkness, will aid the rise.

Parker (1901) found that female *Labidocera* migrate surfacewards at night due to positive phototropism and negative geotropism, and Dice (1914) considered geotropism the major factor in the migration of *Daphnia*. However, the recent findings of Kikuchi (1938) exemplify the fact that the actual rôle played by geotropism probably varies from species to species.

Since *Centropages* is positively phototropic to very low intensities, the upward migration will presumably continue when the light is exceedingly weak. Further, when the animals have reached the surface, they will tend to remain there during darkness owing to the negative geotropism, and they will not take up a more or less uniform distribution, as Russell has supposed for some planktonic species.

As regards the downward migration in the morning, we were generally unable to demonstrate repulsion with increase in light intensity using electric light in the laboratory. However, in the experiments using direct sunlight, it was shown that increase in intensity at a low intensity range from about 700 to 3,500 f.c., did cause repulsion, and this range of light change might be expected in the early morning. It is possible that exposure to darkness during the night might also tend to render the animals more sensitive to light, but there is the opposing geotropism to consider. This has been shown, however, to be definitely weaker for average light intensities. Further experiments, however, are desirable in this connection.

Although no experiments were conducted to test specifically Esterly's theory of a diurnal rhythm (Esterly, 1917, 1919), it would seem from an examination of our readings at different times of the day that such a rhythm is absent in *Centropages*. Rose considers that a species exhibiting diurnal vertical migration is adapted to a certain optimum light intensity (Rose, 1925). Many investigators have been unable to demonstrate such optima in the laboratory. Esterly, for example, found *Calanus* negative to all intensities used, provided the temperature was above 10° C. Rose believed that if a wide range of intensities was employed in the experiments, the optima would be demonstrable. We therefore used a very wide range in our experiments, but did not find any such optimum for *Centropages*.

Reversal of phototropic signs with absolute intensity of light was also difficult to obtain, though Loeb, Parker, Rose, etc. have demonstrated this for many planktonic species. It should be noted that Clarke also found there was no evidence from his experiments for an optimum light intensity in *Daphnia*. He also found that reversal of phototropic sign could not be brought about by absolute light intensity in this form. (Clarke, 1930 and 1932.)

Various authors have frequently pointed out the complexity of the problem of vertical migration by showing differences in behaviour between different species (e.g. Clarke, 1933), between the sexes of a single species (e.g. Russell, 1928), and between ages of the same sex of one species (e.g. Gardiner, 1933). The observations of the authors of the present paper further illustrate that although the majority of adult female *Centropages typicus* do behave in a similar manner, variation in vertical distribution between individuals may be expected even when they are of the same species, sex and age. This is in agreement with field studies.

SUMMARY

Experiments on phototropism and geotropism in adult female *Centropages typicus* were conducted. The following conclusions were indicated:

A. Experiments with experimental tube horizontal.

1. The copepods are primarily photopositive and constant exposure does not modify this reaction except at very high intensities in the neighborhood of that of bright sunlight (*ca.* 12,000 foot-candles) when a large number exhibited negative phototropism after continual exposure for about an hour.
2. The lowest intensity at which there were always more copepods in the brighter than the darker half of the tube was *ca.* 0.005 f.c.
3. There are two types of individuals. One type, after continuous exposure to light, becomes indifferent. In the other type, the animals are persistently attracted.
4. Decrease in light intensity, at a variety of rates and at a wide range of intensities, always results in increased attraction.
5. Increase in light intensity, at a variety of rates and at a wide range of intensities, has no effect on the behaviour. Only prolonged exposure at high intensities repels the animals.

B. Experiments with experimental tube vertical.

1. With the light from above the animals stay mainly at the top of the tube through a wide range of intensities, a distribution which is probably the result of positive phototropism, negative geotropism, or both.
2. Increases in intensity have no effect on the animals except when sunlight is used. A fair percentage of the animals is then repelled.
3. With the exception of decreases as low as 10 per cent per hour, decreases in intensity result in increased attraction.
4. The animals are strongly negatively geotropic in darkness. When geotropism and phototropism are opposed, the reactions depend upon the intensity of the light.
5. The possible bearing of these conclusions on the vertical distribution and diurnal vertical migration of adult female *Centropages typicus* is discussed.

BIBLIOGRAPHY

CLARKE, G. L., 1930. Change of phototropic and geotropic signs in Daphnia induced by changes of light intensity. *Jour. Exper. Biol.*, **7**: 109–131.

——, —. —., 1932. Quantitative aspects of the change of phototropic sign in Daphnia. *Jour. Exper. Biol.*, **9**: 180–211.

CLARKE, G. L., 1933. Diurnal migrations of plankton in the Gulf of Maine and its correlation with changes in submarine irradiation. *Biol. Bull.*, **65**: 402–436.

DICE, L. R., 1914. The factors determining the vertical movements of Daphnia. *Jour. Animal Behavior*, **4**: 229–265.

ESTERLY, C. O., 1917. The occurrence of a rhythm in the geotropism of two species of plankton copepods when certain recurring external conditions are absent. *Univ. Calif. Publ. Zool.*, **16**: 393–400.

——, —. —., 1919. Reactions of various plankton animals with reference to their diurnal migrations. *Univ. Calif. Publ. Zool.*, **19**: 1–83.

GARDINER, A. C., 1932. Vertical distribution in Calanus finmarchicus. *Jour. Mar. Biol. Ass'n., N.S.*, **18**: 575–628.

JOHNSON, W. H., 1938. The effect of light on the vertical movements of Acartia clausi (Giesbrecht). *Biol. Bull.*, **75**: 106–118.

KIKUCHI, K., 1938. Studies on the vertical distribution of the plankton Crustacea. *Records of Oceanogr. Works in Japan*, **10**: 17–41.

LOEB, J., 1908. Über Heliotropismus und die periodischen Tiefenbewegungen pelagischer Tiere. *Biol. Zentral.*, **28**: 732–736.

PARKER, G. H., 1901. The reactions of copepods to various stimuli and the bearing of this on daily depth-migrations. *Bull. U.S. Bur. Fish.*, **21**: 103–123.

RUSSELL, F. S., 1928. The vertical distribution of marine macroplankton. VII. Observations on the behavior of Calanus finmarchicus. *Jour. Mar. Biol. Ass'n., N.S.*, **15**: 429–454.

ROSE, M., 1925. Contribution à l'étude de la biologie du plankton. Le problème des migrations verticales journalières. *Arch. de Zool. expér. et gén.*, **64**: 387–542.

Contribution No. 208

Reprinted from THE AMERICAN JOURNAL OF PHYSIOLOGY
Vol. 126, No. 2, June, 1939

RENAL AND VASCULAR RESPONSES TO EPINEPHRINE INJECTIONS IN GLOMERULAR AND AGLOMERULAR FISH[1]

LOUIS A. TOTH

From the Woods Hole Oceanographic Institution,[2] Woods Hole, Mass.; the Department of Physiology, School of Medicine and Dentistry, University of Rochester, Rochester, New York; the Laboratory of Physiology, Tulane University School of Medicine, New Orleans, La.

Received for publication March 21, 1939

Infusions of epinephrine in anesthetized dogs result in either an oliguria or a polyuria depending on the rate at which the infusions are made (1). A possible explanation for the dual effect of epinephrine can be advanced from the work of Richards and Plant (2) and Winton (3), who suggested that with a low concentration of epinephrine in the blood stream the efferent arterioles are constricted and induce polyuria; but with a higher blood concentration after large injections the afferent, or both the afferent and efferent, arterioles are constricted, producing oliguria. In order to determine the rôle of the glomerulus in the urinary response to epinephrine the present investigation was undertaken.

METHODS. The puffer (Spheriodes maculatus) possessing a glomerular kidney, and the toadfish (Opsanus tau) possessing an aglomerular kidney (4), were used in the experiments. The animal was anesthetized by placing it in a urethane solution in sea water (1 per cent for the puffer; 2 per cent for the toadfish) and then was transferred to a more dilute urethane solution (0.5 per cent for the puffer; 1.0 per cent for the toadfish). It was pinned on its back with its gills under water and with oxygen bubbling through the water, or directly through the mouth and over the gills. The temperature of the water was constant within 2.0°C. during any one experiment. One ureter was cannulated and the urine flow determined by frequent observations of the meniscus in the cannula; the urine rate was later plotted as cu. mm. per 100 grams body weight per hour (cu. mm./100 grams BW/hr.). The blood pressure in the coeliac or subclavian artery was determined in several experiments with a mercury manometer, 10 per cent sodium citrate being used as the anticoagulant in the manometer. The heart rate was counted in the majority of the experiments. All of the injections were made through a cannulated gonadal vein.

---

[1] A preliminary report of this work appeared in the Proceedings of the Society for Experimental Biology and Medicine, **38**: 299, 1938.

[2] Contribution no. 208.

After determining a normal urine rate, dilute sea water equivalent in volume to that of the epinephrine solution to be used subsequently was injected as the control. The volume never exceeded one cubic centimeter. When the effects of the control solution had worn off the epinephrine solution (Parke-Davis Adrenaline Chloride) varying in concentration from 1:1000 to 1:50,000 in dilute sea water, was injected and the response of the urine rate, blood pressure and heart rate observed and recorded.

Results. The results of one of the experiments on the puffer are given in figure 1. At *B* 0.5 cc. of the control solution was injected. No significant change occurred in the urine rate or the blood pressure. The heart rate as a rule did not vary greatly; but in this experiment the decrease in heart rate just before the injection of the control solution was evidently the result of asphyxia because after the oxygen flow was increased at *A* the heart recovered. This response of the asphyxiated heart to oxygen was observed in a number of animals.

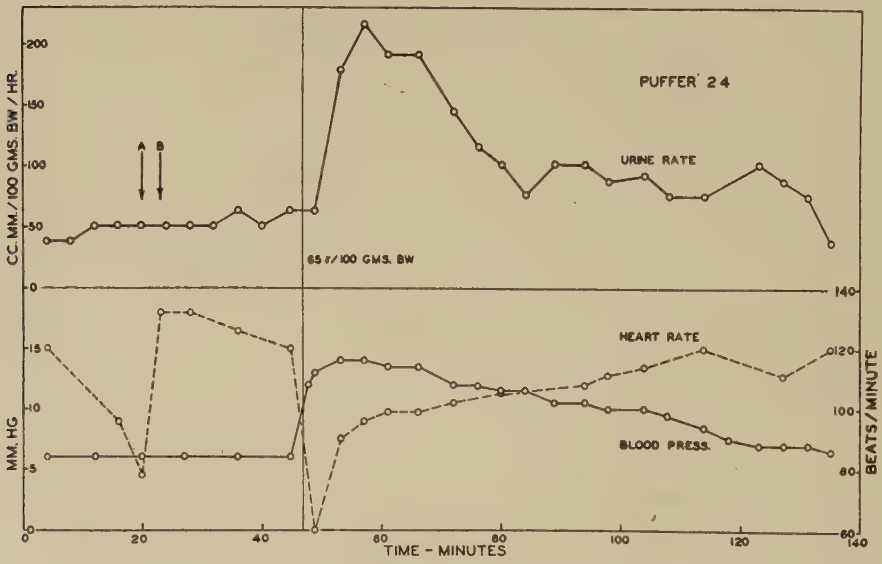


Fig. 1. Urine, arterial blood pressure, and heart rate responses of the puffer to control and epinephrine injections.

In contrast to the control solution the urine rate after epinephrine increased significantly, an increase of 340 per cent occurring in puffer 24. The blood pressure also increased even though the heart rate fell from 120 to 60 beats per minute. This fall in heart rate usually occurred after every epinephrine injection.

A summary of the urine and cardio-vascular responses in the experi-

TABLE 1

Urine and cardio-vascular responses to epinephrine and control injections in the puffer (Speriodes maculatus)

ANIMAL NUMBER	WEIGHT	DOSAGE	PREVIOUS URINE RATE	URINE RESPONSE TO:		CARDIAC RESPONSE IN BEATS PER MINUTE* TO:					
				Epineph.	Control	Epineph.			Control		
						1	2	3	1	2	3
	grams	*γ/100 grams body wt.*	*cu. mm./100 grams BW/hour*	*per cent*†	*per cent*†						
20	165	242	122	280	100	117	100	114			
19	156	160	3	11,600	100	36	60	64	50	50	
18	247	105	3	9,500	100	44	36	76	52	40	
14	134	75	35	930	170	42	36	42	62	46	22
17	144	70	6	535	230	62	32	60	64	70	60
24	153	65	51	390	100	124	60	120			
3	160	63	26	1,960	250						
1	177	57	21	525	260						
21	217	46	50	215	150	100	48	90	90	74	84
16	250	40	3	2,360	400	96	62	86	84	88	100
9b	152	32		1,880		84	48	68			
15	198	25	55	330	240	86	66	90	90	90	76
6	241	21	26	690	190	90	42	88			
9a	152	16	5	980	100	54	42	80			
8	228	11	11	3,860	100	64	62	70	50	28	42
7	237	10	5	690	820	86	76	84	22	38	84
12a	163	6	31	265	110	82	56	84	84	82	80
10	195	5	4	3,275		76	24	72			
12c		3		490		72	66	76			
23	203	0	39								

ANIMAL NUMBER	WEIGHT	DOSAGE	BLOOD PRESSURE RESPONSE IN MM. Hg* TO:						CARDIAC RESPONSE IN BEATS PER MINUTE* TO:					
			Epineph.			Control			Epineph.			Control		
			1	2	3	1	2	3	1	2	3	1	2	3
24	153	65	6	14	7	6	6	6						
21	217	46	9	18	11	11	13	7						
22a	219	23	16	29	13	13	13	13	82	78	96	100	102	94
22b		23	13	17	15	16	17	16	88	78	94			
22c		23	15	25	12				100	70	96			

Where several injections were made in one animal they are indicated by a letter after the number identifying the animal.

* In columns 1 are listed the arterial blood pressures and heart rates just preceding the injection; in columns 2 the greatest changes that occurred after the injection; in columns 3 the readings after recovery.

† Per cent of urine rate just preceding injection.

ments carried out on the puffer is given in table 1. In every case the urinary response to epinephrine is much greater than the response to an equal volume of the control solution. In some cases a 100-fold increase in the urine rate occurred, these tremendous increases occurring in those experiments in which the urine rates before the injection were low. At no time did a pronounced oliguria occur, even with the larger doses of epinephrine, as it did in dogs (1). In a few of the experiments not listed no urine flow was evident for 30 minutes before, or after, the injection of the control solution; but after the epinephrine injection a polyuria resulted.

The urine and cardio-vascular responses of the toadfish are given in figure 2. Simultaneous determinations of urine rate, blood pressure, and heart rate were not carried out on the same animal; therefore, the experiments performed on two animals weighing the same and receiving approximately the same amount of epinephrine are given in this figure. The effects of the control injection on urine rate in toadfish 4 are not shown but the increase was from 22 cu. mm. to 25 cu. mm./100 grams BW/hour. The urinary response to the epinephrine solution in this animal was even smaller. The blood pressure response of toadfish 17 to the control solution (injected at *B*) and to the epinephrine, and the heart rate response to the epinephrine are also shown. The heart rate usually increased after both solutions, the increase being slightly greater after the epinephrine. This response is in contrast to that of the puffer.

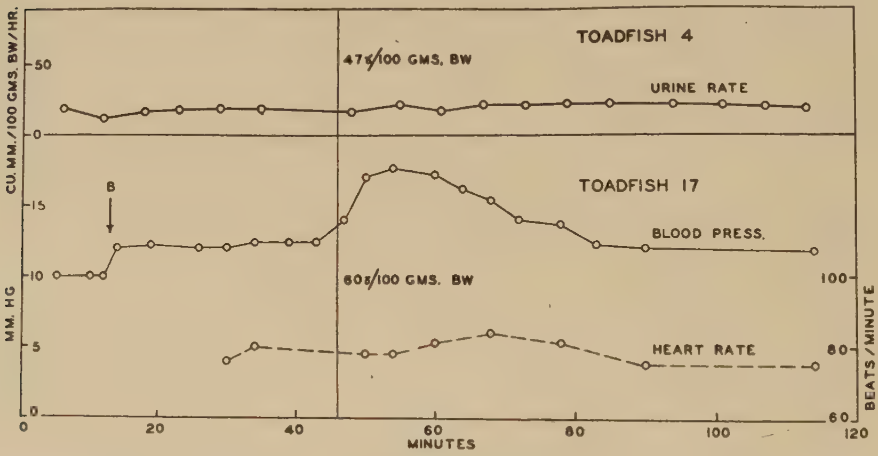


Fig. 2. Urine, arterial blood pressure, and heart rate responses of the toadfish to control and epinephrine injections.

Table 2 summarizes the urine and cardio-vascular responses of the toadfish to the control and epinephrine solutions. There is no great difference in the urine response to the two solutions, a point differing significantly from the response of the glomerular kidney of the puffer. Unlike Bieter's (5) results, at no time did the toadfish show a prolonged and significant polyuria after the epinephrine injections. Bieter reported that magnesium chloride, magnesium sulfate, sodium sulfate, and urea injected intravenously induced a polyuria, and attributed this response to the increased secretion of these substances by the tubules. Evidently the mode of action of the salts in Beiter's work and the epinephrine in the present work is different.

TABLE 2

Urine and cardio-vascular responses to epinephrine and control injections in the toadfish (Opsanus tau)

ANIMAL NUMBER	WEIGHT	DOSAGE	PREVIOUS URINE RATE	URINE RESPONSE TO:		CARDIAC RESPONSE IN BEATS PER MINUTE† TO:					
				Epineph.	Control	Epineph.			Control		
						1	2	3	1	2	3
	grams	*γ/100 grams body wt.*	*cu. mm./ 100 grams BW/hour*	*per cent**	*per cent**						
11	298	67	6	150	165	24	50	30	26	32	30
12a	328	61	10	130	170	58	60	50	74	64	72
6	343	58	3	125	260	42	44	34	52	48	54
7	360	56	3	135		48	54	50			
10	368	55	9	65	100	54	60	66	56	60	56
5	406	49	2	100		34	40	38			
13	420	48	3	270	135	60	66	60	56	58	50
4	423	47	21	110	115	56	60	60	60	60	60
8a	504	40	4	125	100	58	66	58	62	66	58
12b	328	15		80		46	36	40			
9	351	14	13	80	125	30	28	28	60	46	56
8b	504	10		80		44	54	36			
14	402	5	11	120	165	56	60	56	50	56	52
15	415	0	25								

ANIMAL NUMBER	WEIGHT	DOSAGE	BLOOD PRESSURE RESPONSE IN MM. Hg† TO:						CARDIAC RESPONSE IN BEATS PER MINUTE† TO:					
			Epineph.			Control			Epineph.			Control		
			1	2	3	1	2	3	1	2	3	1	2	3
17	420	60	12	18	11	10	12	12	80	78	76			
16	438	23	12	16	13	9	12	12	68	78	84	68	66	68

Where several injections were made in one animal they are indicated by a letter after the number identifying the animal.

* Per cent of urine rate just preceding injection.

† In columns 1 are listed the arterial blood pressures and heart rates just preceding the injection; in columns 2 the greatest changes that occurred after the injection; in columns 3 the readings after recovery.

The urine rates of the anesthetized puffer and toadfish here reported are similar to those reported by Grafflin (6) for the sculpin and toadfish. Calculated as cubic centimeter per kilogram body weight per day he reported the urine rate for the sculpin to be usually less than 4 cc., and that for the toadfish to be below 2.5 cc. From a review of the literature Grafflin gave the rates for other marine teleosts as follows: wrymouth, 1.5 to 11.0 cc., sculpin, 3.2 to 57.0 cc.; goosefish, 12.9 to 54.4 cc.; toadfish, 0.6 to 9.4 cc. According to Grafflin the higher rates are the result of possible injury to the fish due to handling.

COMMENT. Although epinephrine injections induced a rise in the arterial blood pressure in both species of fish used in the experiments, the urinary response differed in that the glomerular kidney showed a polyuria while the aglomerular kidney showed no significant change from that of the control injection. This difference in the urinary response may be correlated with the presence or absence of the glomerulus and its arterioles. With the afferent and efferent arterioles present the renal mechanism which responds specifically to epinephrine gives one of the responses, namely, a polyuria, that the dog's kidney gave (1). Without the glomerulus and its arterioles no significant changes occur after epinephrine injections. Unlike that observed in the dog (1) a persistent oliguria was not observed in the experiments on the glomerular kidney, even with very large doses of the drug.

The cardiac response of the puffer to epinephrine is similar to the findings of Lutz (7), who reported that epinephrine in concentrations of 1:50,000 to 1:25,000 in the immersion fluid produced a slowing or temporary complete inhibition of the beat of the isolated sinus-auricle preparation of Elasmobranch fish. He explains the inhibition as the response of an unbalanced parasympathetic mechanism in a heart which lacks a sympathetic accelerator innervation. This explanation may hold for the puffer but the toadfish seldom exhibited a cardiac slowing.

It is not inferred that marine teleosts and mammals, or even species in the same order of teleosts, respond alike to epinephrine. Nevertheless, the data obtained in the present series of experiments suggest that the polyuria of epinephrine may be of wholly circulatory origin, and not dependent on any activity of the renal epithelium.

SUMMARY

Intravenous epinephrine injections varying in doses from 242 to 3 micrograms per 100 grams body weight in the puffer (Spheriodes maculatus) possessing glomerular kidneys resulted in a polyuria; similar injections in the toadfish (Opsanus tau) possessing aglomerular kidneys, in which the dose varied from 67 to 5 micrograms per 100 grams body weight resulted in no significant polyuria. Both species showed a rise in arterial

blood pressure, but the heart rate of the puffer decreased significantly while the heart rate of the toadfish increased slightly. The hypothesis is advanced that the glomerulus with its afferent and efferent arterioles is necessary for the epinephrine polyuria to occur.

The author wishes to express his gratitude to Dr. E. F. Adolph and Dr. H. S. Mayerson for their helpful criticisms in the preparation of this manuscript; and to Dr. Henry B. Bigelow, Director of the Woods Hole Oceanographic Institution, for having been permitted to do the experiments at the Institution.

REFERENCES

(1) Toth, L. A. This Journal **119**: 140, 1937.
(2) Richards, A. N. and O. H. Plant. This Journal **59**: 191, 1922.
(3) Winton, F. R. J. Physiol. **73**: 151, 1931.
(4) Marshall, E. K. Bull. Johns Hopkins Hosp. **45**: 95, 1929.
(5) Bieter, R. N. J. Pharmacol and Exper. Therap. **43**: 399, 1931.
(6) Grafflin, A. L. This Journal **97**: 602, 1931.
(7) Lutz, B. R. This Journal **94**: 135, 1930.

Contribution No. 209

[From AMERICAN JOURNAL OF SCIENCE, VOL. 237, NOV., 1939, PP. 798-810]

MINERALS FROM DEEP SEA CORES AND SURFACE DEPOSITS OF BERMUDIAN CALCAREOUS SEDIMENTS.*

JOHN A. YOUNG, JR.

ABSTRACT. The lithologic characteristics and mineralogy of the deep sea sediments brought up by five cores taken near Bermuda from depths ranging from 1,320 meters to 3,338 meters are discussed. The insoluble mineral content of these sediments is compared with the mineral content of the eolianites and of modern beach and dune sands. The origin of the various minerals found is discussed, and a theory is proposed to account for the occurrence on Bermuda of several minerals undoubtedly foreign in origin.

INTRODUCTION.

THIS paper is concerned with a study of the minerals from a set of cores taken from the sea bottom on the flanks of the Bermuda platform, a comparison of these minerals with those found by Larsen on the island of Bermuda, and a consideration of their probable origins.

Bermuda is of special interest for such a study inasmuch as the only rocks known to exist in the immediate vicinity, other than the calcareous sediments derived from the products of lime-secreting organisms, are a series of volcanic rocks differentiated from a parent subsilicic alkalic magma. No quartz or minerals of continental origin, such as andalusite, staurolite, or cyanite, would be expected. As a result of the boring of the deep well in 1912, it is known that weathered volcanics occur within at least 245 feet of sea level, and relatively unaltered volcanic material within 530 feet of the surface,[1] and possibly even higher. Since the level of the sea was probably lowered about 90 meters, or 295 feet,[2] during the Pleistocene, the volcanic material was undoubtedly subjected to relatively recent wave action. The continual kneading of the waves during the changes of sea level would tend gradually to mix the vol-

---

* Contribution No. 209 of the Woods Hole Oceanographic Institution.
Contribution No. 211 of the Department of Mineralogy and Petrography, Harvard University.

[1] Pirsson, L. V.: Geology of Bermuda island, This Journal, Vol. 38, pp. 191-192, 1914.

[2] Daly, R. A.: The changing world of the ice age, p. 48, New Haven, Connecticut, 1934.

canic minerals with the calcareous sediments so common around the island.

The material examined was collected by Mr. Henry C. Stetson on a trip of the "Atlantis" to Bermuda in 1935. The samples were obtained by means of a weighted coring tube. The locations of the stations are shown on the accompanying map,

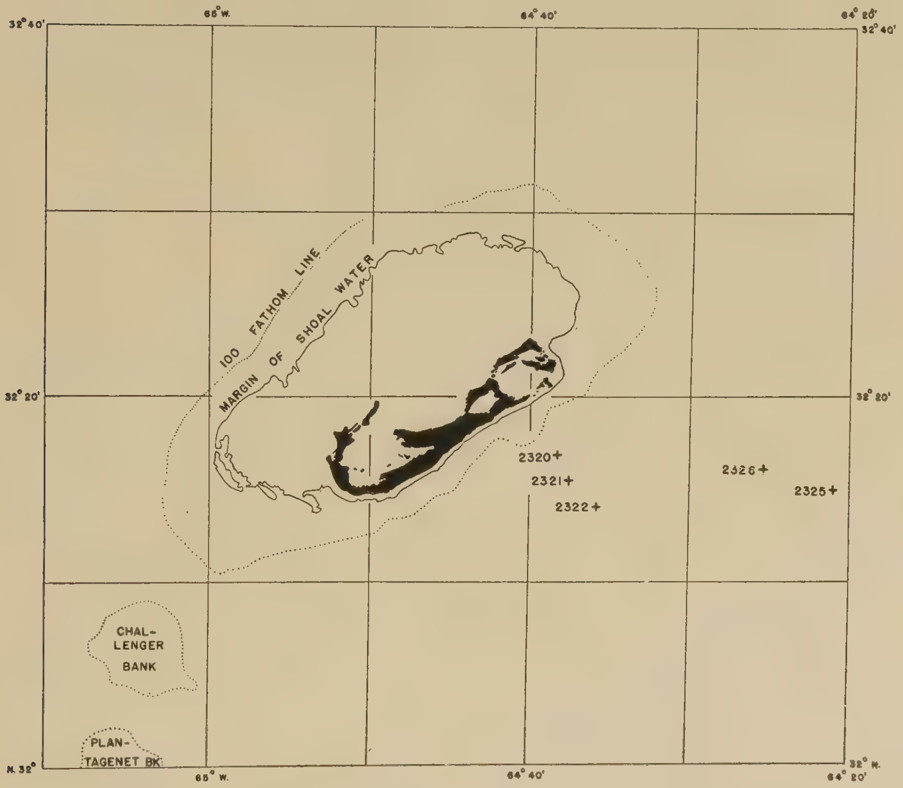

65° W.
64° 40'
64° 20'
32° 40'
32° 40'
32° 20'
32° 20'
100 FATHOM LINE
MARGIN OF SHOAL WATER
2320
2321
2322
2326
2325
CHAL-LENGER BANK
PLAN-TAGENET BK.
N. 32°
32° N.
65° W.
64° 40'
64° 20'

Fig. 1. Key map of Bermuda showing locations of stations.

Fig. 1. The core numbers given in this paper are the Woods Hole Oceanographic Institution's station numbers. The letter suffixes indicate whether the sample came from the top (T), middle (M), or bottom (B) of the core. The cores varied from one foot to three feet in length.

The writer expresses his sincere thanks to Mr. Henry C. Stetson for furnishing the material upon which this study was made, and for the data upon which the discussion of the characteristics of the sediments is based. The writer also thanks Dr. Esper S. Larsen and Mr. Stetson for their many helpful suggestions during the course of the work on this problem.

THE SEDIMENTS.

The data concerning the nature of the sediments as derived from the cores were very kindly furnished by Mr. H. C. Stetson. The samples were collected from depths ranging from 1,320 to 3,338 meters. The material is predominantly of detrital calcareous substance, with varying proportions of skeletons of lime-secreting organisms, and insoluble material, largely inorganic. It is of fairly fine grain. Sponge spicules compose most of the organic insoluble residue; the inorganic insolubles are discussed later in this paper.

Core 2,320, taken from a depth of 1,320 meters, is 37 centimeters long. Its components appear to be homogeneous from top to bottom. A few coccoliths are present, but are very rare. Mechanical and partial chemical analyses show (diameters in microns):—

	Q_1	M	Q_3	So	Sk	log Sk	$CaCO_3$
2320T	8.1	3.6	2.0	2.1	1.26	.1	82.16%
2320B	50.0	28.0	7.5	2.59	.48	—.3188	84.62

The coarse material at the bottom of the core appears to be entirely of fragments of calcareous algae, bryozoans, and worm tubes, characteristic of the reef which surrounds the island. The median diameter of 2,320T, as shown in the above results, is consequent upon the presence in the sediment of numerous tests of foraminifera.

Core 2,321, from a depth of 1,780 meters, is 23 centimeters long. The upper 18½ centimeters is a brown mud, separated by a sharp break from the remaining 4½ centimeters of blue material. The top and bottom material is all of about the same size. Mechanical analyses (diameters in microns) and partial chemical analyses by Gonyer show:—

	Q_1	M	Q_3	So	Sk	log Sk	Caco$_3$	$MgCO_3$
2321T	18.5	6.1	2.1	2.97	1.05	.02	64.64%	3.84%
2321B	25.0	6.5	2.7	3.05	1.46	.16	62.00	4.01

The size of the median is controlled largely by the sizes of the coccoliths and foraminifera present in the sample. The combined percentages of calcium and magnesium carbonates represent approximately the total solubles. The low carbonate percentages in this core are due to the presence of a relatively large amount of insoluble material, a large proportion of which is of clay sizes.

Core 2,322 was taken from a depth of 2,370 meters, and is but 10 centimeters long. The upper 2 centimeters was yellowish and granular in appearance. It is made up of coccoliths and coccospheres with a smaller proportion of organic particles. The lower 8 centimeters is finer grained, brownish, and consists almost wholly of organic particles. A few coccoliths are present. The insoluble minerals were studied only from a sample taken from the top of this core. Partial chemical analyses by Gonyer show:—

	$CaCO_3$	$MgCO_3$
2322T	90.14%	4.44%
2322B	93.65	2.24

Core 2,325, taken from a depth of 3,338 meters, is 37.5 centimeters long. The top .5 centimeters is a calcareous layer very rich in coccospheres with a few coccoliths and a very few radiolarians. The next 9.5 centimeters is much coarser than the lower portion, and contains considerable inorganic material, largely of volcanic origin. The lower 27.5 centimeters is yellowish, has a great abundance of coccoliths, with the coccospheres most numerous. A few radiolarians are present. Mechanical and partial chemical analyses show (diameters in microns):—

	Q_1	M	Q_3	So	Sk	log Sk	$CaCO_3$
2325T	510.0	240.0	50.0	3.2	.449	—.3478	58.23%
2325B	8.1	5.4	3.1	1.62	.86	—.0655	68.60

The large grain sizes of the volcanic layer are reflected in the mechanical analysis. The low $CaCO_3$ content is due to the high percentage of volcanic minerals in this layer. The results of the mechanical analysis of 2,325B are a reflection of the sizes of the coccoliths and coccospheres.

Core 2,326, taken from a depth of 2,880 meters, is 69 centimeters in length. It appears to be homogeneous in texture from top to bottom, although the bottom 10 or 12 centimeters are distinctly darker in color. The upper portion is pure chalk white. The core consists almost entirely of coccoliths, with an occasional coccosphere intact. Rhabdoliths are rare and no rhabdospheres were found. The coarse portion separated in the mechanical analysis of 2,326B consists almost entirely of foraminifera. A little reef material is also present. The mechanical analyses show (diameters in microns):—

	Q_1	M	Q_3	So	Sk	log Sk
2326T	36.0	3.6	1.6	4.75	4.46	.65
2326B	53.0	28.0	5.2	3.2	.352	—.45

Here again the mechanical analysis is a direct reflection of the sizes of unworn organic particles, and not primarily of detrital material. Chemical determinations by Gonyer show:—

	$CaCO_3$	$MgCO_3$
2326T	93.09%	1.57%
33cm. below top	95.37	1.56
51cm. below top	93.80	1.54
2326B	88.34	1.56

The lower $CaCO_3$ content of 2,326B is due to the presence of the fine-grained clayey material which gives the lower 10 or 12 centimeters its darker color.

MINERALOGY.

Samples were taken from both top and bottom of each core and their mineral content carefully examined. Each sample was first examined for the presence of insoluble minerals, such as zeolites. The samples were then treated with hydrochloric acid, and the insoluble residues examined. The amount of insoluble material in the sediments varied considerably, but in all the samples except 2,325T it was less than one per cent. In some samples magnetic and heavy separations were used to facilitate the study, but quantitative results of these separations were not recorded. Table I shows the results of the mineralogical study. About a score of minerals were determined, and their characteristics are discussed below.

Quartz.

Quartz is present in most of the samples studied, but in very small amount. In general, the smaller fragments, average size 0.1 mm. in diameter, are sharply angular, whereas the larger grains, average size about 0.3 mm. in diameter, are subangular, irregularly pitted, and apparently polished. The larger grains are characteristic of the beach and dune sands, while the smaller angular grains are more common in the deep sea sediments. The subangular variety predominates in core samples

TABLE I.

Insoluble Minerals.

	Quartz	Orthoclase	Plagioclase	Microcline	Feldspar (unidentified)	Hornblende	Brown Biotite	Green Biotite	Pyroxene	Glauconite	Magnetite	Perovskite	Sphene	Zircon	Spinel	Phillipsite	Serpentine	Brown Garnet	Amorphous ferric oxides	Apatite	Volcanic Rock	Volcanic Glass
2320T	S	S		T	S		T	T	C	S		T	T	T			T	T	S		C	
2320B	S	S			S	T	S	T	S	S	T		T						S		S	
2321T		C	S		S	T	C	T	S	S	T	S	T	T					C	T	C	
2321M	T	S	S	T	S	T	T	T	S	S		S	T	T	T				S		D	
2321B	S	C	C		S		S	S	S	C		S		T					S		C	T
2322T	T						T		T		T	T									D	T
2325T		S	T		S	T	S		C	A	A	S	T			S		T	S	S		
2325B	T	S	T		T	T	S		C	C	C	T	T	T	T	T	T				A	
2326T	S	S	T		T		T	T	S	C						T					D	
2326B	*	*			*	*	*		*	*				*		*	*			*		
Modern Beach Sand	39.1%				1.8%				36.1%		3.0%	16.9%			1.2%				1.8%			
Modern Dune Sand	51.9%				5.2%	0.6%			28.0%		2.0%	6.5%							2.6%			

Note: D, dominant, indicates 50% or over of total insolubles; A, abundant, 20% to 50%; C, common, 5% to 20%; S, scarce, 1% to 5%; and T, trace, less than 1%. Core #2320 contains over 50% of siliceous organic remains. Most, if not all, of the pyroxene is augite. * Indicates present, sample too small to give accurate estimate of amount.

2,326T and 2,326B, however. Larsen[3] found quartz to be the most common mineral in the insoluble residues from both the soils and the eolianites of Bermuda. Inasmuch as that island rests on the top of an extinct volcano which exuded subsilicic lavas and which apparently rises from the floor of the oceanic basin, no quartz-bearing rocks are believed to exist in this region. We must therefore look for foreign sources for the origin of the quartz, and possibly several other minerals whose source may not have been the island or its submarine platform. The source of these foreign minerals will be discussed elsewhere in this paper.

Feldspar.

Feldspars are in no instance abundant constituents of any of the samples studied, although only one sample lacks individual grains of members of this group, and that sample is composed almost entirely of fragments of a fine-grained, slightly altered, volcanic rock which appears to be made up almost entirely of orthoclase and oligoclase crystals. Orthoclase is the most numerous of the feldspar fragments in the sediments, and a plagioclase near oligoclase is next in abundance. Several small angular microcline fragments showing characteristic grid twinning structure were found. Much-altered fragments of feldspar which can not be determined are present in all but the sample noted above; most, however, are surprisingly fresh. The average size is about 0.2 mm. in diameter, although one large microcline grain measured 0.45 mm. x 0.36 mm. Larsen[4] and Pirsson[5] both reported orthoclase in the results of their respective studies, but Larsen found only one per cent of plagioclase in the insoluble residue from the soils and none from the eolianites, whereas Pirsson reported no plagioclase at all. The orthoclase grains in the sediments are undoubtedly derived from the volcanic rock of the island. The plagioclase is also probably local in origin, since oligoclase as well as orthoclase was found in some of the volcanic rock fragments. Microcline is probably foreign to the island.

---

[3] Sayles, Robert W.: Bermuda during the ice age, Proc. Am. Acad. of Arts and Sciences, Vol. 66, pp. 439-444, 1931.

[4] Sayles, Robert W.: op. cit.

[5] Pirsson, L. V.: Geology of Bermuda island; the igneous platform, This Journal, Vol. 38, pp. 189-206 and 331-334, 1914.

Hornblende and *Biotite.*

Neither hornblende nor biotite is an important constituent of any of the samples. The hornblende, where present, is a green variety, pleochroic from bluish green to yellowish green, and is present only in small grains. No hornblende was found in any of the fragments of volcanic rock, and Pirsson did not find any in the rock fragments from the deep well. Larsen cited a trace from one soil locality only. Hornblende is, as Sayles mentioned, probably foreign.

Brown biotite is the more important of the two micas present, occurring in all the cores. Many of the flakes are zoned, the color a more intense brown toward the outer margin. Inclusions of minute, colorless, needle-like crystals resembling apatite are common. Brown biotite is for the most part in small flakes about 0.3 mm. in diameter, although several with diameters from 2 to 3 mm. were seen. Green biotite is not as abundant as the brown variety, and occurs chiefly in smaller flakes. Pirsson noted brown biotite as a constituent of some of the volcanics, but not the green. Brown biotite is undoubtedly of local origin; the green variety may have altered from the brown[6] as the first transition stage in the alteration to glauconite.

Pyroxene.

The study of the pyroxene formed one of the most interesting aspects of this work. Well over half the fragments are characterized by the pointed, spine-like projections parallel to the elongation of the grains as noted by Larsen[7] in his study of the Bermuda soils. (See Fig. 2.) This feature is present in the pyroxene from all the cores, whereas the pyroxene grains from the dune and beach sands show evidence that serrate edges have been present, but the points have, for the most part, been broken and rounded. The origin of this feature was puzzling, until finally a small fragment of fine-grained volcanic rock was found containing two phenocrysts of spiny pyroxene, proving the primary origin of this serrate characteristic. The pyroxene is somewhat variable in its properties, ranging from colorless to the characteristic purplish brown of the titanoaugites. Dispersion is present in all the pyroxenes and is most marked in those of deepest color. The mean index of refraction is near 1.72. The optic sign is invariably positive. The grains are uniform in size, ranging from 0.2 mm. to 0.3 mm. The pyroxenes all appear to be of local origin.

---

[6] Galliher, E. W.: Glauconite genesis, Geol. Soc. Am., Bull. 46, p. 1355, 1935.

[7] Sayles, Robert W.: op. cit., p. 440.

Glauconite.

Glauconite is present in varying amount in all the samples except 2,322T. In general, a brown altered form predominates. Glauconite is commonly formed on the sea bottom, and is possibly derived from the alteration of biotite according to the theory of E. W. Galliher.[8] Its source is therefore local.

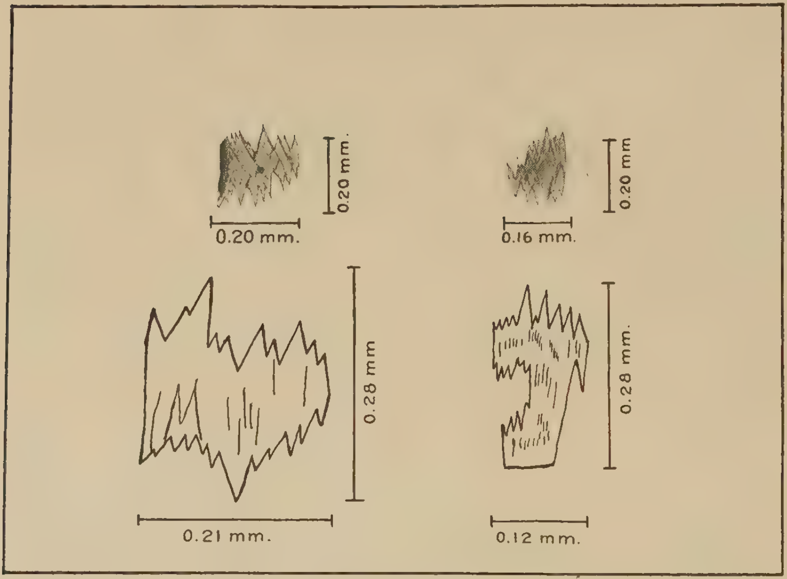


Fig. 2. Photomicrographs and camera lucida drawings of typical pyroxene grains showing spine-like projections.

Accessory Minerals.

The common igneous rock accessory minerals found are magnetite, perovskite, sphene, zircon, spinel, garnet, apatite, and fluorite. Of these, magnetite and perovskite are the most common, as one or the other or both are found in every core and sand sample. They were also found by Larsen in most of his soil samples and in the eolianites. Pirsson identified perovskite with black marginal alterations in a section of the lamprophyric lavas, and also noticed in the melilite basalt fragments yellowish masses of granular sphene, which he believed to be an alteration product derived from perovskite. Perovskite is a characteristic accessory mineral of subsilicic alkalic rocks. Perovskite and magnetite are both undoubtedly local in origin.

---

[8] Galliher, E. W.: op. cit.

Sphene is present in clear yellowish grains, some of which showed several crystal faces. Small doubly-terminated crystals and rounded grains of zircon are present in many of the samples. Colorless spinel and brown garnet are both rare. Apatite is rare, except in 2,325T, and where present, the grains are well-rounded. Apatite may also be present as the small needle-like inclusions in the biotite flakes, already mentioned. Several small, angular grains of purple fluorite were distinguished in 2,326B, but were noticed in no other sample. Sphene and brown garnet were found by Larsen in both soils and eolianites. The sphene, brown garnet, and apatite could have been derived from the volcanic rocks, as could the spinel. The apatite, because of its concentration in 2,325T, is believed to have a local source. Zircon and fluorite are common accessory minerals of alkalic rocks, and their source could also be local. The rounded grains of zircon may have been foreign.

Phillipsite.

Phillipsite has long been known as a constituent of deep sea sediments.[9] It was found in several of the samples as very minute, doubly terminated crystals. The form is identical with that shown in the photomicrograph by Murray and Renard. The crystals are rarely twinned, however. Phillipsite, when in deep sea deposits, is believed to be formed at the ocean bottom as a result of the decomposition of augitic lava.

Miscellaneous Minerals.

In addition to the minerals already mentioned, varying amounts of serpentine, chlorite, andalusite, and amorphous brown to red hydroxides of iron were found. Several aggregates of fibrous sepentine were noted in three of the cores. Pirsson also found sepentine which he believed to be an alteration product of olivine from the olivine-bearing melilite basalt. A trace of chlorite was found in one sample, and a single grain of andalusite in another. Both chlorite and andalusite are of negligible importance. Iron oxides were found in the majority of the samples, and in some they form irregular masses up to 5 mm. in diameter. These oxides are probably derived locally as alteration products of the iron-bearing minerals of the volcanic rocks.

---

[9] Murray, J., and Renard, A. F.: Challenger Report, Deep Sea Deposits, pp. 400-411, 1891.

Volcanic Material.

Volcanic material, as either glass or aggregates of fine-grained crystalline material, is present in all cores. A small amount of brown glass was found, and this in but two cores. Fragments of a fine-grained, sanidine-bearing, trachytic, volcanic rock were found in all cores. It was in this rock that the augite phenocrysts were found. A sodic plagioclase feldspar near oligoclase was noticed in many of these fragments. The grains are sub-angular to rounded in outline, and are composed almost entirely of small crystals of sanidine, and needle-like crystals of plagioclase. In some samples, the grains are uniformly fresh, whereas in others they are considerably altered. No quartz was identified in any of the rock fragments. The various members of the volcanic series underlying Bermuda undoubtedly served as the source of the igneous material.

Comparison of Mineralogy of Surface and Deep Sea Deposits.

By putting together the results of this study and those of Larsen on the mineralogy of the soils and eolianites, it is found that certain minerals are characteristic of each type of deposit, whereas others are common to both. The results are tabulated below.

Minerals common to both surface and deep sea deposits	Minerals found only in surface deposits	Minerals found only in deep sea deposits
quartz	rutile	microcline
orthoclase	red garnet	glauconite
plagioclase	hydrargillite?	phillipsite
hornblende	tourmaline	serpentine
biotite	epidote	apatite
pyroxene	muscovite	volcanic rock*
brown garnet	corundum?	andalusite
magnetite	cyanite	
perovskite	staurolite	
zircon		
spinel		
sphene		
volcanic glass*		
amorphous iron oxides*		
chlorite		

* indicates substances other than minerals

All the minerals in the first column with the probable exception of quartz are ones which we would expect to have been derived from the type of volcanic rocks underlying the island. In the second column, all the minerals except the red garnet and hydrargillite? are present in but small quantities only. The red garnet could easily have been derived from the volcanic rocks. The hydrargillite? was formed in place in the soils.[10] The identification of the corundum was not definite enough to base any conclusions on its presence. Epidote might be derived from the volcanics. It seems doubtful that any of the remaining minerals of the second column are local in origin. Among the minerals of the deep sea deposits, glauconite and phillipsite were undoubtedly formed on the floor of the ocean. The apatite, serpentine, and volcanic rock are probably from the volcanics of the island. The place of origin of the microcline is in doubt. Andalusite must have been foreign.

Source of Foreign Minerals.

Sayles mentions three possible origins for the foreign minerals found in Bermuda. They are: (1) transportation in the crops and intestinal tracts of migratory birds which use Bermuda as a stopping place in their seasonal migrations, (2) tropical hurricanes, and (3) transportation by planktonic jelly-like forms of life or by the sargasso weed common on Bermuda shores. There is, of course, the possibility that the quartz crystallized in an as yet undiscovered silicic differentiate of the parent sub-silicic alkalic magma. The recent dust storms in this country have emphasized the importance of the transportation of sand and dust by the wind. Page and Chapman[11] studied samples from the dustfall of December 15-16, 1933, and found that material up to 150 microns in diameter had been carried at least 1500 miles by the wind. Their results are conclusive, as they show that previous to the dust storm, practically the entire region east of the Mississippi River was covered by snow, and that the source of the material must have been somewhere in the western mid-continent region or in the southwestern states. Winchell and Miller[12] studied material carried by the dust storm of March 7-10, 1918, and reported grains as coarse as 2 mm. The distance travelled by this coarse material is unknown, but the source could not have been local, as the region in the immediate vicinity of Madison, Wisconsin, where the samples were collected, was covered by snow at the time of the dustfall. It is therefore conceivable that material could have been transported the 600 miles from the continent to Bermuda by wind. It is possible that a large amount of the foreign material may have been transported to Bermuda during the Pleistocene glacial periods when the wind velocities were much greater, due to the unstable conditions of the atmosphere at that time.[13]

---

[10] Larsen, E. S.: Personal communication.

[11] Page, L. R., and Chapman, R. W.: The dustfall of December, 15-16, 1933, This Journal, Vol. 28, pp. 288-297, 1934.

[12] Winchell, A. N., and Miller, E. R.: The dustfall of March 9, 1918, This Journal, Vol. 46, pp. 599-609, 1918.

Conclusions.

The minerals found can be separated into three distinct groups, those of local derivation, those that are authigenic, and those that have been introduced. It seems apparent that biotite, pyroxene, some if not all of the minerals of the accessory group, serpentine, possibly hornblende, and the feldspars, with the possible exception of microcline, could have been derived from the volcanic series underlying the islands. Phillipsite, glauconite, and the oxides of iron were probably formed by chemical alteration reactions on the sea bottom from the minerals derived from the volcanic rocks. The only mineral of any importance for whose origin it seems necessary to look elsewhere is quartz, although this also may have been derived from some hidden quartz-bearing volcanic rock.

---

[13] Bryan, Kirk, and Cady, R. C.: The Pleistocene climate of Bermuda, This Journal, Vol. 27, pp. 241-264, 1934.

DEPARTMENT OF MINERALOGY AND PETROGRAPHY,
HARVARD UNIVERSITY,
CAMBRIDGE, MASS.

Contribution No. 210

Reprinted from BIOLOGICAL BULLETIN, Vol. LXXVI, No. 3, 305–324, June, 1939
Printed in U. S. A.

NOTES ON THE FAUNA ABOVE MUD BOTTOMS IN DEEP WATER IN THE GULF OF MAINE[1]

HENRY B. BIGELOW AND WILLIAM C. SCHROEDER

(*From the Woods Hole Oceanographic Institution, Woods Hole, Massachusetts*)

INTRODUCTION

It has long been known that the waters just above bottom, in the mud-floored depressions of the western side of the Gulf of Maine at depths of 70–90 meters, are the home of an abundant population of the large edible shrimp, *Pandalus borealis,* accompanied by the smaller species, *P. montagui, P. propinquus* and *Dichelopandalus leptoceros* (Rathbun, 1883, p. 142; 1884, p. 819). After the introduction of the otter trawl to the Gulf of Maine waters, small amounts of these shrimps were landed from time to time in New England ports, and experimental trawling by the General Sea Foods Corporation in 1927–1928 again revealed the presence of *P. borealis* and its companion species in commercial quantities in the deep bowl just north of Cape Ann (Birdseye, 1928). But exploitation failed to follow, although Hjort's explorations of 1897 and 1898 (Hjort and Ruud, 1938) had long before led to the development of an extensive fishery in the other side of the Atlantic, which has gradually expanded to all suitable localities around the coasts of Norway.

Investigations by Hjort and Ruud (1938) and by Broch (1935) had also shown that *P. borealis* is but one member of a distinctive faunal community, some of the members of which live on bottom, others in the waters close above. Information from various sources had similarly shown that the *Pandalus* of the Gulf of Maine have as companions the same species of flat fishes, of rose fish (*Sebastes*), and of rockling (*Enchelyopus*), as in Norway, as well as several gadoids (*Merluccius, Urophycis*), which while peculiar to American waters, are at least similar to gadoid members of the Norwegian shrimp community. Hjort and Ruud's successive explorations had further demonstrated that *Pandalus* occurs in greatest abundance in situations where the bottom waters are sufficiently quiescent for organic debris to settle to the bottom.

---

[1] Contribution No. 210 from the Woods Hole Oceanographic Institution.

The presence of similar faunal assemblages living under conditions presumably the same in the two sides of the Atlantic opens interesting problems of environmental control. The Woods Hole Oceanographic Institution, therefore, welcomed the opportunity, in August, 1936, to make a further survey of the Gulf of Maine shrimp grounds with " Atlantis," under Professor Hjort's personal supervision, and with the assistance of Captain Hagbart Høium, an experienced Norwegian shrimp trawler.

The purpose of the investigation being primarily to explore the abundance of *Pandalus* and of associated fishes in a favorable environment, most of the hauls were made in the bowl north of Cape Ann and west of Jeffrey's Ledge (Area *A,* Fig. 1), where shrimps were already known to be plentiful, and which resembles the Norwegian shrimp grounds in its fjord-like topography and considerable depth. For comparative purposes, hauls were also made in the northeastern and southwestern branches of the open basin of the Gulf (Areas *B, C,* Fig. 1). Corings of the bottom for chemical analyses were obtained at thirteen of the stations.

The catches were so encouraging from the fisheries standpoint, that the exploration of the local shrimp stock was continued during the following two months by local fisheries interests—again under the supervision of Professor Hjort and of Captain Høium.

The present report on the regional distribution of the more prominent members of the *Pandalus* community is a sequel to Hjort and Ruud's (1938) preliminary report, and to Walford's (1936) discussion of the prospects of the shrimp fishery that appears now to be in the process of development.

Methods

The hauls (with two exceptions) were made with otter trawls of the sort used in the Norwegian shrimp fishery, brought by Professor Hjort from Norway for the purpose, the distinctive feature of which is that the footrope works about six inches above the bottom to avoid catching mud, with a sweep rope suspended below (for detailed description, see Walford, 1936). The success of the cruise was largely due to Captain Høium's skill in their use. One trial was also made with the footrope scraping the bottom. The mesh-size of the Norwegian nets was 1¾ inches (stretched) throughout. But four sizes of trawl were employed, their footropes respectively 35, 76, 82, and 117 feet in length, and the hauls varied in duration from 30 to 90 minutes, at an average speed of 1.5 knots. It has therefore been necessary to adjust the catches to a common standard, for comparative purposes, a 60-minute haul with 82-foot trawl being chosen as the procedure most often followed during the cruise. Unfortunately, this adjustment is only a rough approximation, because the precise outline assumed by an otter trawl depends on a variety of factors such as speed, angle of the boards, and the type of bottom over which it is being drawn. The present calculation is based on the assumption that the breadths of sweep of trawls with footropes of different lengths are in the same ratios as semicircles of corresponding perimeters.

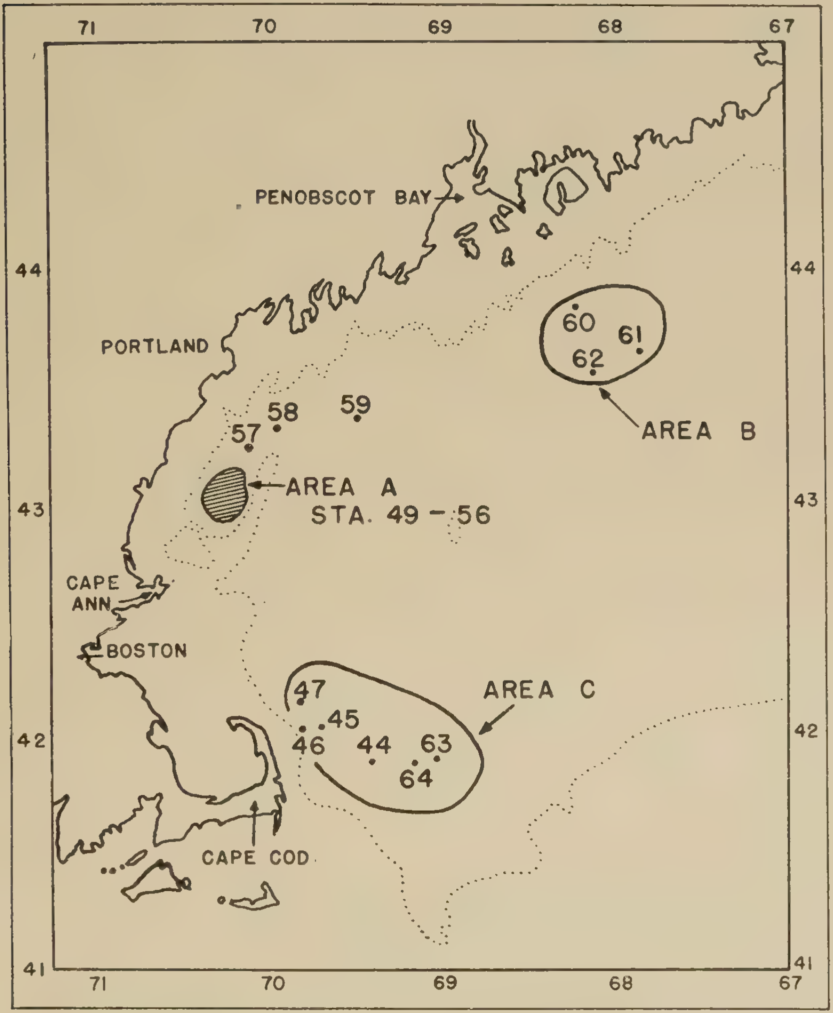

71
70
69
68
67
44
43
42
41
PENOBSCOT BAY
PORTLAND
60
61
62
AREA B
58
59
57
AREA A
STA. 49 – 56
CAPE ANN
BOSTON
47
45
46
44
63
64
AREA C
CAPE COD

FIG. 1. Chart of western part of the Gulf of Maine, showing locations of "Atlantis" stations 2644–2664, August 18–23, 1936.

The chemical procedure, for which our thanks are due to Dr. S. A. Waksman, consisted of analyses of the upper half-inch of each core, for carbon, by the chromic acid oxidation method, and for total nitrogen by a semi-micro-Kjeldahl method. These were carried out at the New Jersey Agricultural Experiment Station at New Brunswick, New Jersey. Measurements were also made at Woods Hole of percentage loss on ignition, but showed considerable irregularity. Since this loss does not represent the organic fraction alone, but also such water as is driven off from the clay fraction at high temperatures, these values are not included in the present discussion.

TABLE I

Catches of the more prominent species at each station, adjusted as above (p. 306). Numbers italicized are derived from approximate counts.

Station	Depth	Amounts of Pandalus in liters	Numbers of Sebastes	Numbers of Merluccius	Numbers of Hippoglossoides	Numbers of Glyptocephalus	Numbers of Urophycis tenuis	Numbers of other fish‡
2644	200	5	*108*	15	0	0	11	6
2645	183	2	16	8	0	2	3	4
2646	144	2	*432*	*240*	2	0	65	4
2647	228	1	3	1	0	0	7	11
2649	164	32	150	*700*	12	10	32	2
2650*	175	24	*224*	338	4	1	36	0
2651*	168	11	*131*	*262*	3	2	6	1
2652	160	71	*168*	*196*	13	14	39	1
2653†	155	168	107	20	47	24	28	34
2654	158	126	183	*840*	13	35	11	2
2655	168	100	*150*	*225*	13	3	40	2
2656	177	56	*283*	*351*	63	12	23	7
2657*a*	120	2	*100*	*160*	5	0	*20*	1
2657*b*	120	3	*103*	*67*	17	8	*40*	2
2658*a*	162	16	*400*	*467*	9	1	*67*	4
2658*b*	163	50	*450*	*600*	10	5	0	3
2659*a*	164	48	*150*	*600*	24	12	50	6
2659*b*	164	27	*188*	*700*	13	9	70	3
2660	192	1	250	300	26	18	100	14
2662	198	1	270	100	0	2	0	5
2663	183	4	833	*200*	5	0	47	39
2664	215	1	*67*	47	0	0	12	7

* Net damaged, calculations assume that only half the catch was saved.
† In this haul, the footrope scraped the bottom.
‡ See Table II.

Qualitative Composition of the Community

The most interesting aspects of the catches from the qualitative standpoint are that the number of species taken in abundance at any given station was so small (Table I), and that the same few species dominated, in all three areas visited, as well as at intervening locations. Among the catches of shrimps, for example, only occasional specimens of other related species, or of Pasiphaea, were noted among the more plentiful *P. borealis.* In fact, the latter so predominates among the shrimp population in deep water in the Gulf that a sample taken at random from catches made at depths greater than 160 meters in the Jeffrey's Bowl, in the summer of 1938, consisted of 738 specimens of *P. borealis,* but only 9 of all other pandalids combined. In shoaler water, however, in that general vicinity, the relationship is the reverse, as off Casco Bay in 30–40 meters, and at a neighboring station in about 90 meters, where *P. propinquus* greatly predominated over *P. borealis* (39 to 0 and 39 to 1 respectively) at that same time. This is in line with Rathbun's (1883, p. 143) statement that while *P. montagui* and *Dichelopandalus leptoceros* are often associated with *P. borealis* over soft bottoms, they are not only the most plentiful in shoaler water, but occur on gravelly and sandy bottoms as well as on mud.

TABLE II

List of "various" fishes other than those recorded in Table I, trawled on bottom in Jeffrey's Bowl and in the open basin of the Gulf of Maine, during August, 1936.

Species	Jeffrey's Bowl	Open basin
Myxine glutinosa	x	x
Squalus acanthias	x	x
Raia senta	x	
Raia stabuliforis	x	x
Raia scabrata	x	x
Clupea harengus	x	x
Artediellus uncinatus	x	
Cyclopterus lumpus	x	
Lumpenus lampetraeformis	x	
Cryptacanthodes maculatus	x	x
Pollachius virens		x
Gadus callarias	x	x
Melanogrammus aeglefinus		x
Urophycis chuss	x	x
Urophycis chesteri		x
Enchelyopus cimbrius	x	x
Brosme brosme		x
Macrourus bairdii		x
Lophius americanus		x

Our catches of fishes, in August, 1936, were similarly dominated by a group of 5 species, in combination, namely: by rose fish (*Sebastes marinus*), silver hake (*Merluccius bilinearis*), hake (*Urophycis tenuis*) and flat fishes (*Glyptocephalus cynoglossus* and *Hippoglossoides platessoides*), and to such an extent that the total catch of about 11,900 fish included only 183 specimens of all the other species combined, that are included in Table II. The total list of 24 species together with a few others that have been picked up in deep trawlings previously (*Argentina, Triglops, Cottunculus, Aspidophoroides, Liparis, Pholis, Leptoclinus, Zoarces, Lycenchelys*) includes the great majority of the members of the Gulf of Maine fish fauna that are to be expected on the floor of the deep troughs, whether as regular inhabitants or stragglers. This is a very much less varied assemblage than inhabits the corresponding depth zone along the offshore slope of the Gulf of Maine and of southern New England (for complete list of records there, see Goode and Bean, 1896).

Regional Distribution

Regional segregation of the catches (Table III) shows that shrimps were taken in much greater average abundance in the deepest part of the Jeffrey's Bowl (Area *A*) and on the northern slope of its northern rim (Station 2658, 163 meters) than in either branch of the main basin of the Gulf (Areas *B, C*).

TABLE III

Regional distribution of average catches.

Area	Hauls	Shrimp	Sebastes	Merluccius	Flat fish	Urophycis	Various fishes	Total fishes
	Number	Liters	Numbers	Numbers	Numbers	Numbers	Numbers	Numbers
A	7	60	187	416	28	26	2	649
B	2	1	260	200	23	50	10	543
C	6	2	243	92	2	34	12	383
St. 2658	2	33	425	534	13	0	5	977

From the environmental standpoint, the outstanding feature of this Bowl is the fjord-like character given to its deepest parts (170–192 meters), by the shallow ridge of Jeffrey's Ledge to the south and offshore, and on the north, by a sill with a maximum depth of about 134–137 meters (Fig. 2). This enclosure appears to be more effective, so far as concerns the activity of circulation of the bottom waters, than the topography of the sill might suggest, for temperature averages some 1–2° colder in midsummer in the bottom of the trough than at corresponding depths in the open basin to the east of the barrier, only a few miles distant.

Hjort and Ruud (1938, p. 103) have already pointed out that the mud was richest in carbon and in nitrogen where large catches of shrimps were made. This is corroborated by the following comparisons of the catch of shrimps with the percentages of organic carbon and of nitrogen in the corings (Table IV), the average being 4.02 per cent of organic matter for the group of stations where the catch of shrimps was more than 30 liters, but only 3.05 per cent for stations yielding 5 liters of shrimps, or less.

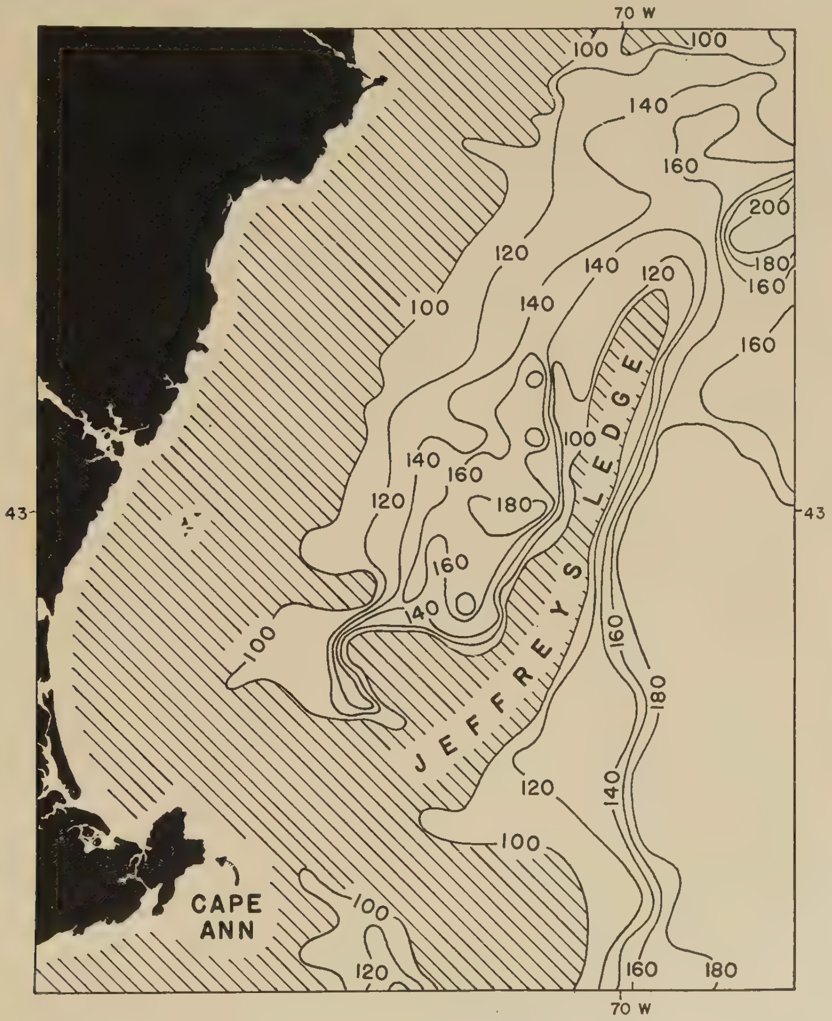

70 W
100
100
140
160
200
180
160
160
120
140
120
100
140
JEFFREYS LEDGE
100
140
160
120
180
160
140
100
160
180
120
140
100
CAPE
ANN
100
120
160
180
70 W
43
43

Fig. 2. Submarine topography of the region between Jeffrey's Ledge and the western coast-line of the Gulf of Maine at depths greater than 100 meters.

At one station (2662), it is true, where the percentage of organic matter was high, the catch of shrimps was very small; regional irregularities are, in fact, to be expected, in the nature of the case. But in no instance was the mud poor in organic content where shrimps were abundant. While the correlation is not so close between the catches of shrimps and the percentage of nitrogen, the latter averaged 0.338 per cent for the rich and 0.234 per cent for the poor shrimp stations. In other words, the average percentage of organic carbon was about one-third higher, and that of nitrogen about one-half higher where catches of shrimp were relatively large than where they were small. Unfortunately, the data do not afford so satisfactory a comparison from the regional standpoint, because the mud was sampled at only two of the stations in the deeper part of the Jeffrey's Bowl. At each of these (Stations 2649, 2654), however, the percentage of organic carbon closely approached the maximum found at any station, while the percentages of nitrogen (0.295 and 0.309 per cent) were at least somewhat above the average for the series as a whole (0.262 per cent). It is interesting that the station that was the richest of all, both in organic carbon and nitrogen (Station 2658) was at least moderately productive of shrimps, though located north of the sill. Thus, it seems sufficiently established, both for Norwegian waters and for the Gulf of Maine, that in summer *Pandalus* is abundant only in situations where organic matter is plentiful on the sea floor below; and by available evidence this applies to the males throughout the year. But the fact that considerable catches of ovigerous individuals were landed by fishermen from depths of 70–90 meters only, in the northwestern side of the Gulf, during the winter of 1938 suggests that the large females tend to work inshore into shoaler and more turbulent situations during the egg-bearing period.

TABLE IV

Percentage of organic matter and of nitrogen in dry mud and catch of *Pandalus*.

Station	Shrimps	Organic matter*	Nitrogen
	liters	*per cent*	*per cent*
2654	126	4.1	0.309
2659	37 av.	3.7	0.195
2658	33 av.	4.2	0.553
2649	32	4.1	0.295
2644	5	2.6	0.311
2663	4	2.6	0.115
2657	2.5 av.	2.4	0.201
2645	2	3.7	0.217
2647	1	3.1	0.205
2660	1	3.3	0.301
2662	1	4.0	0.310†
2664	1	2.8	0.217

* Carbon X 1.724.
† Determination made at Woods Hole.

It seems that we are dealing here with a food relationship, for while no direct observations are available as to the diet of *Pandalus* in the Gulf of Maine, Wollebaeck (1903, see also Hjort and Ruud, 1938, p. 60) found the stomachs of this shrimp in Norwegian waters to contain animal remains of various origins, among a mass of indeterminate mud, evidence that while it feeds on bottom, its diet consists of the remnants of dead organisms or perhaps of bacteria and protozoa, rather than of the mud itself. This is in line with Waksman's (1933) demonstration that the organic matter in the mud is largely in the form of humus, and hence not likely to be readily digestible by the higher animals.

The catches of *Merluccius* also averaged considerably larger in Area *A* and at the neighboring station (2658) than in either of the other areas, though there is no reason to suppose that the type of bottom is of direct influence in this case, but rather that the significant parallelism is between the number of fish and of shrimps, as discussed below. *Sebastes,* on the other hand, averaged somewhat less plentiful in the Jeffrey's Bowl (Area *A*) than over the rim of the latter (Station 2658) or in the open basin (Areas *B* and *C*). But the difference in average catch from area to area was so small for pleuronectids and for *Urophycis* that it may not have been regionally significant.

Among the fishes of minor numerical importance, *Enchelyopus cimbrius* and *Urophycis chuss* were encountered at so many stations (respectively 13 and 12 hauls out of 22), that they appear practically universal over the deep bottoms both of the Jeffrey's Bowl and of the western branch of the open basin of the Gulf, though the maximum catch was only 9 specimens in the one case, 10 in the other. *Enchelyopus* was also taken in the eastern basin, and failure to take *U. chuss* there in our few hauls is no evidence that it does not actually occur there.

Odd specimens of all other species included in Table II, and listed on page 309, have also been taken in the bottom of the Jeffrey's Bowl at depths greater than 160 meters on one occasion or another, with the exceptions of *Triglops, Argentina, Aspidophoroides, Pholis, Leptoclinus, Brosme, Urophycis chesteri, Macrourus, Lophius,* haddock and American pollock. These are also to be expected there, either because plentiful in somewhat shoaler water in the near vicinity, or because already known to occur in deep water elsewhere in the Gulf. Arctic species in particular, such as *Cottunculus,* would be as likely to maintain a small population in the low temperatures of the Bowl as anywhere else to the west of Cape Sable.

In short, there is nothing in the available data to suggest that the sill responsible for the fjord-like character of this Bowl gives any distinctive character to the fish fauna of its bottom waters, as contrasted with that of the open basin of the Gulf to the eastward. At most, certain species that have their center of abundance over the slope outside the Gulf (*Macrourus, Urophycis chesteri, Argentina*) may be progressively less numerous westward, until they reach the trough only as stragglers, if at all; whereas certain others may be most plentiful there, whether because of cold water affinity, or to utilize the particular food supply provided by the local abundance of *Pandalus,* as appears to be the case with *Merluccius.*

Urophycis tenuis has long been known to feed chiefly on shrimp (see Bigelow and Welsh, 1925, p. 450, for summary of its feeding habits); in fact, all but one of the specimens of this species that were opened during our cruise contained more or less remnants of large *Pandalus.* But the following tabulation (Table V) fails to suggest any correlation between the numbers of *Urophycis* and the amounts of shrimp taken, for the average catch of the former averaged about the same for the nine stations which yielded 24 liters or more of shrimps, as for the ten stations that yielded 5 liters or less (34 and 37 *Urophycis,* respectively), while the largest and the smallest catches of *Urophycis* were each made at a station where shrimps were very scarce.

TABLE V

Numerical relationship of fish to shrimps.

Shrimps, liters	126	100	71	56	54	48	32	27	24	16	11	5	4	3	2	2	2	1	1	1	1
U. tenuis, numbers......	11	30	40	26	0	50	34	75	36	67	6	23	60	40	4	86	20	14	100	0	19
Sebastes, numbers.......	183	150	168	283	450	150	150	188	224	400	131	108	833	103	16	432	100	3	250	270	67
Flat fish, 2 sp., numbers..	48	16	25	75	15	36	22	22	6	10	5	0	5	25	2	2	5	44	2	2	0
Merluccius, numbers.....	840	225	196	351	600	600	700	700	338	467	262	15	200	67	8	240	160	1	300	100	47

The catches of *Sebastes* seem also to have been independent of those of shrimps, the average being almost exactly the same for the group of stations where shrimps were plentiful (20 liters or more), as for the group where they were scarce (216 and 218 *Sebastes*, respectively); while the largest and smallest catches of *Sebastes* (833 and 3) were both made at stations yielding only 4 liters and only 1 liter of shrimps, respectively. Neither do the present data yield any information as to the extent to which *Pandalus*, when abundant, serves as prey for *Sebastes*, the great majority of the latter having regurgitated the stomach contents before they were brought on board.

A rough parallelism does, however, appear, between the abundance of *Merluccius* and of shrimps, illustrated by the facts that the catch of the former averaged four times as great (494) for the group of stations where shrimps were abundant as where they were scarce (114); that it was only where the catch of shrimps was less than 6 liters that the catch of *Merluccius* was as small as 100; and that no hauls where shrimps were so scarce yielded as many *Merluccius* as the average for the series as a whole (306). To judge from the predaceous nature of this fish and from its independence of the bottom, we are dealing here with a predator-prey relationship, though our present data fail to yield direct information in this regard for *Merluccius* any more than for *Sebastes*, and for the same reason.

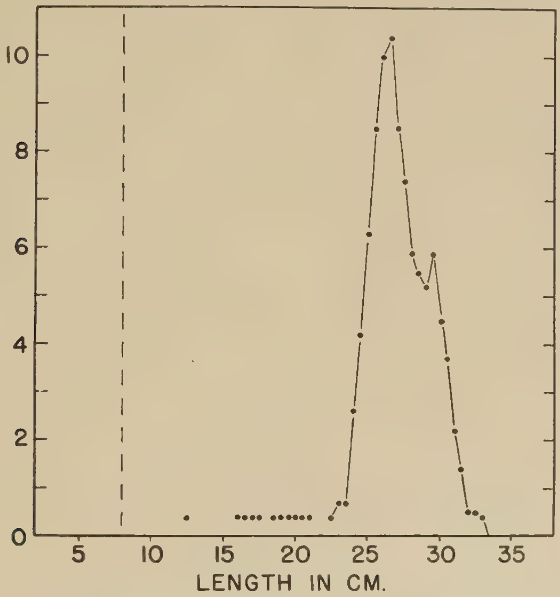


FIG. 3. Length-frequency distribution of 270 specimens of *Sebastes*, Station 2662, smoothed once by running average of three. The broken curve marks the lower limit for adequate sampling by the nets employed.

Flat fishes of the two species, combined, also averaged considerably more plentiful (av. 30 flat fish) where shrimps were in more than moderate abundance than where the catches of shrimps were 5 liters or less (av. 9 flat fish). But there being no reason to suppose that either of these pleuronectids preys to any extent on shrimps, the parallelism in this case suggests that the same muddy bottoms which provide the richest feeding for *Pandalus* are also rich in the small invertebrates on which *Hippoglossoides* and *Glyptocephalus* chiefly subsist. While we have no precise data, in this respect, for the Gulf of Maine, such is certainly true in Norwegian waters, where soft bottoms in similar situations support a wealth of invertebrate life (Broch, 1935; see also Hjort and Ruud, 1938, p. 106).

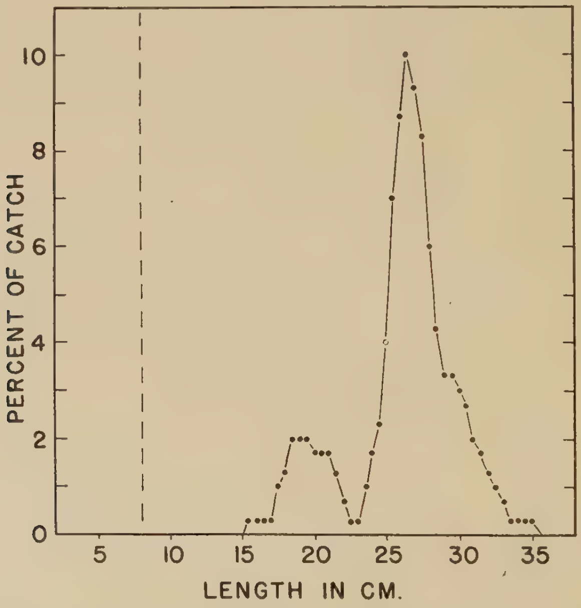


FIG. 4. Length-frequency distribution of 300 specimens of *Sebastes,* Station 2663, smoothed once by running average of three. The broken curve marks the lower limit for adequate sampling by the nets employed.

Size Distribution of Different Species of Fish

It was likely due to the mesh-size of our trawls that the catches of *Pandalus borealis* consisted almost wholly of medium and large-sized individuals, the commonest lengths being from 12 to 18 cm. (rostrum-telson), which covers the upper size range for that species. But this factor cannot be invoked to explain a great scarcity, in the catches of *Sebastes,* of *Urophycis,* and of the two common flat fishes, of the smaller sizes that the mesh might be expected to sample.

In the case of *Sebastes,* the great majority were upwards of 22–23 cm. long, averaging something like 25–30 cm., a size that would be classified as "medium to large" in statistics of the commercial fishery (Figs. 3, 4). In fact, out of a total of 4,334 specimens taken, only 115 were less than 20 cm. long, and only 56 smaller than 15 cm., although the net should certainly have sampled this spiny species adequately down to 7–9 cm., and have taken at least a scattering of still smaller sizes had they been present in numbers at all approaching those of the larger fish. The rate of growth of *Sebastes* in the Gulf of Maine has not been studied, but its pelagic larvae have been taken there up to a length of 2.1 cm. (to a considerably larger size in European waters). The facts that fry of 3.7 to 7.5 cm. are abundant on bottom in spring and summer (Bigelow and Welsh, 1925; Bigelow and Schroeder, 1936) and that in a collection made in summer at Eastport, Maine, many years ago, there is a distinct size group of 5.1–6.3 cm., make it likely that the peak at 7–9 cm. shown on Fig. 5 represents fish one year old, and the next larger group centering at 15–21 cm., those two years old. On this basis, the fish of 24 cm. and larger, that formed the bulk of the catch in all three areas, were at least three years old and upwards. Unfortunately, our data afford no information as to how many year classes were actually included, for these older fish appear as a single size-group on the graphs for the two stations where unselected samples were measured (Figs. 3, 4, Areas *B, C*), while inspection of the fish larger than 20 cm. in Area *A,* as brought on deck, showed that there was no obvious succession of recognizable size-groups among them, either. In other

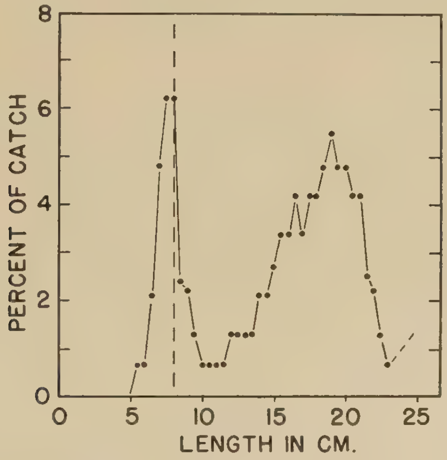


FIG. 5. Length-frequency distribution of all *Sebastes* taken less than 24 cm. long (146 specimens), smoothed once by running average of three. The broken curve marks the lower limit for adequate sampling by the nets employed.

words, it is likely that had the entire catch of more than 4,000 specimens been measured, the resultant graph would have closely resembled Figs. 3, 4. However, since the dominant group includes the sizes that yield commercial catches, we may assume that the greater part of the usual life of the species is included from three years onward—however long that may endure. In fact, occasional specimens of 43–45 cm. are as close an approach to the maximum yet recorded for the Gulf (about 60 cm., Bigelow and Welsh, 1925, p. 305) as was to be expected from so few hauls.

The absence of small sizes is still more striking for *Urophycis tenuis,* for not a single specimen shorter than 21 cm. was taken among a total of 664, ranging up to about 70 cm. in length and to 8 lb. in weight, though the net could be depended upon to take them down to 16–17 cm. Again, in the cases of *Hippoglossoides* and *Glyptocephalus,* the smallest sizes (within the sampling range of the nets, or down to 10–15 cm.) were much less strongly represented than the successively larger sizes (Figs. 6, 7). In fact, *Hippoglossoides* yielded only 21 specimens shorter than 20 cm., and *Glyptocephalus* 17, out of totals of 183 and 135 respectively. If previous estimates of the rates of growth of these two pleuronectids in the Gulf of Maine be correct (Bigelow and Welsh, 1925, pp. 486 and 515; Bigelow and Schroeder, 1936, pp. 340–341), the first size-group of each that was well represented in the catches, centering at about 17–20 cm. for *Glyptocephalus* and at 20–23 cm. for *Hippoglossoides,* was at least two years old—with the yearlings only about one-fourth to one-third as numerous. Or, if Molander's (1925) estimate, based, however, on conditions in the Baltic, applies, the first prominent group of *Glyptocephalus* would be the four-year-olds. The evidence afforded by these two species is especially instructive, because the generality of distribution over the mid-range of included sizes shows that the local stocks had not recently been subject to any outstanding variations in the success of individual year classes.

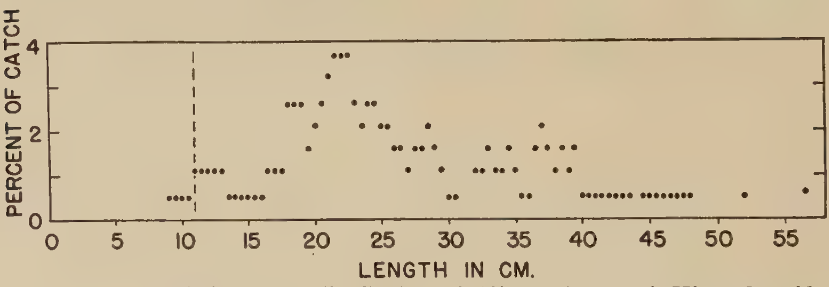


FIG. 6. Length-frequency distribution of 187 specimens of *Hippoglossoides platessoides,* smoothed once by running average of three. The broken curve marks the lower limit for adequate sampling by the nets employed.

In short, our catches contain a very much weaker representation of the first two or more year classes that the nets might be expected adequately to sample of *Sebastes,* of *Urophycis,* and of the two pleuronectids than of the older fish, whereas the reverse would be the expectation in a normal population distribution. Since this applies to four species of widely separated taxonomic groups, differing widely, too, in their life histories, it is safe to assume that we have to do with a general depth or regional relationship, not with a chance irregularity in the relative strengths of individual year classes, such as might have been argued had only one species been at issue. If, then, the year 1936 be acceptable as representative, it appears that this group of fishes does not disperse into the deep troughs of the Gulf until they are at least two or more years old, a conclusion at least compatible with their generally non-migratory nature. The graphs further suggest that such individuals of these species as do stray out into these situations, or descend thither from the upper strata, tend, on the whole, to remain there year after year—or at least that none of these species shows any general tendency to depart thence, with increasing age. This appears also to apply to the few cod that wander out onto these deep soft bottoms, where very large specimens are sometimes caught, but very few small ones.

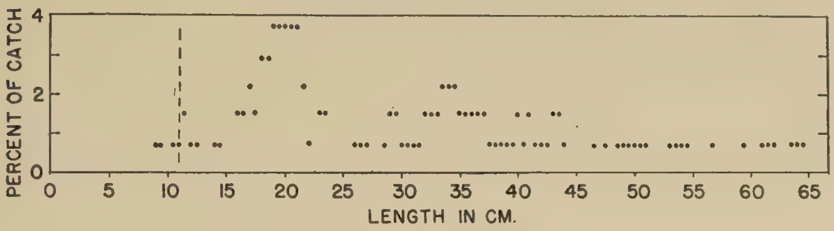


FIG. 7. Length-frequency distribution of 135 specimens of *Glyptocephalus cynoglossus,* smoothed once by running average of three. The broken curve marks the lower limit, for adequate sampling by the nets employed.

In the case of *Merluccius,* however, the catches were strongly dominated by a size group, with a modal length of about 17 cm., with the next longer (and very much less abundant) group centering at about 26 cm. (Fig. 8). Earlier studies (Bigelow and Schroeder, 1936, p. 338) would suggest that the first of these groups represents the fish hatched in the preceding summer, i.e., the yearlings, the second size group being the two-year-olds. Confirmation of this growth schedule for these comparatively cold waters is afforded by the fact that a small lot (28 specimens) taken near Mt. Desert in July, 1930, fell into the same approximate size divisions (15 fish, average, 15 cm.; 13 fish, average, 26 cm.) with no fish between 20 and 23 cm. in length. *Merluccius* of 18–21 cm. taken near Chatham in the same season may best be interpreted as one-year-olds that had grown faster at somewhat higher temperatures. This leaves only the post larvae of the year unaccounted for, among the younger fish. These would be so small (perhaps 2.5–3.5 cm.) in the month in question—if indeed they descend into the bottom waters by that date—that our nets would not have taken them; nor would have until after several months more growth on their part, to judge from the fact that fry trawled by "Albatross II," off Long Beach, New York, in 1928 were only 5.7–11.8 cm. long in November. Thus, *Merluccius* (unlike its companion species) passes its first summer of rapid growth (second summer of life) in great abundance in deep water. The discovery of this habitat for it, combined with captures of this same size group in 18–22 meters near Mt. Desert, and of fish slightly larger in 45–50 meters off Cape Cod (mentioned above), is especially interesting, because previously this age group was close to unknown in the Gulf of Maine, although larvae are produced there in profusion, and larger fish of 20 cm. and upwards occur there in great abundance, both inshore and on the Banks (Bigelow and Welsh, 1925, p. 389). Present findings thus corroborate the earlier suggestion that young *Merluccius* are, in fact, as plentiful in the Gulf as the local abundance of adults would suggest, but that they keep to somewhat deeper water for the most part.

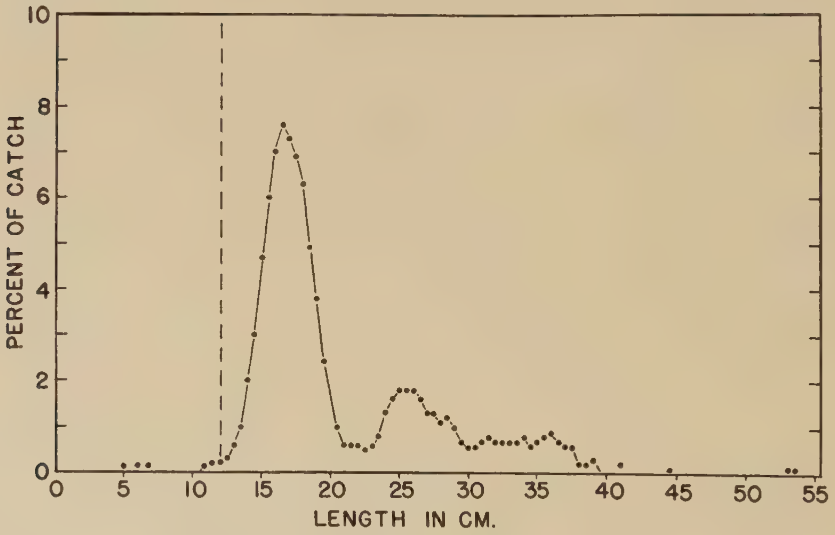


FIG. 8. Length-frequency distribution of 1,088 specimens of *Merluccius bilinearis,* smoothed once by running average of three. The broken curve marks the lower limit, for adequate sampling by the nets employed.

It appears, however, that most of the juvenile *Merluccius* that find their way out, or down, into the troughs, remain there through one summer of growth only, else our hauls might have been expected to have yielded a much larger proportion of the next larger, and of subsequent size groups than was actually the case. Whether their subsequent departure takes place in the following autumn as part of the migration out of the Gulf of Maine, with which the silver hake is generally credited (Bigelow and Welsh, 1925, p. 388), or whether the troughs actually serve as wintering grounds for at least a part of the Gulf of Maine stock, must remain an open question, until these localities are explored during the cold months. We may, however, point out that the latter alternative would at least be compatible with the temperature cycle. The water at 150–170 meters is coldest in spring and summer, both in the Jeffrey's Bowl (2.5–4.5°) and in the western branch of the western basin (4.5–6°), warmest in late autumn or early winter (5–7° and 6–8°, respectively), while deeper still, in the basin the seasonal range is normally less than 1.0° (see Bigelow, 1927, Figs. 5, 6, 70, 72).

In any case, it now seems established that in subsequent feeding seasons most of the *Merluccius* that inhabit or visit the Gulf, repair to shoaler waters either on the Banks or around the coastal slope, to prey on the young fry of various other fishes.

Amounts of Pandalus and Fish Combined

Finally, speculation is perhaps permissible as to the total mass of animals, of a size our nets would sample, that exists in summer in the water next to bottom, in the rich shrimp area in the Jeffrey's Bowl. In this connection we have first to consider how much (if at all) the catches were impoverished by the failure of the nets to strain the water immediately in contact with the bottom. Our only direct evidence in this respect is the difference between catches in the standard hauls made with raised footrope, and in the one haul in which the footrope swept bottom (Station 2653), which yielded at the rate (adjusted) of 107 *Sebastes,* 20 *Merluccius,* 71 flat fish, 33 *Urophycis,* 34 " various " fishes, and 168 liters of *Pandalus.* This contrasts with an average of 377 *Sebastes,* 713 *Merluccius,* 32 flat fish, 49 *Urophycis,* 7 " various " fishes, and 99 liters of shrimps, for the three most productive catches of each of these categories with raised footrope, and with a maximum of 450 *Sebastes,* 846 *Merluccius,* 75 flat fish, 86 *Urophycis,* 11 " various " fishes, and 126 liters of shrimps for any one haul of the latter type in the same general area (Area *A,* Fig. 1). On this basis, it appears that inclusion of the six inches of water next the bottom might well have raised the average catch of shrimps in this region (the richest shrimp ground) by anywhere from one-third to two-thirds. Some increase in the catch of flat fish might also have resulted; and this last is made the more probable by the fact that Birdseye's (1928) twelve experimental hauls in the same region made with trawls of the usual pattern (footrope on bottom) yielded a somewhat greater weight of large flat fish of the two species in question (average, 275 lb.) than of shrimps (average, 217 lb.), whereas the reverse was true [2] for our hauls with raised footrope. But there is nothing to suggest that the catches of the more active and more plentiful fishes were significantly reduced by our failure to sample the few inches of water that is in immediate contact with the sea floor. If anything the reverse is suggested, perhaps because the stirring of the mud by the trawl gives the fish warning of its approach. And these three species—*Merluccius, Sebastes,* and *Urophycis*—made up the major weight of fishes caught.

Assuming that, by actually sweeping the bottom, the average catch would have been increased by 50 per cent for shrimp, and by 30 per cent for flat fishes of the two species combined, but that the catches of the other major species of fish would not have been materially affected, the average for the Jeffrey's Bowl, deeper than 150 meters would be 37 flat fish, 187 *Sebastes,* 416 *Merluccius,* 26 *Urophycis,* 2 odd fishes, and 90 liters of *Pandalus.* Crediting the latter with an average weight of 0.97 lb. per liter as determined by measurements made on board, and using conversion factors of 1 lb. per fish for *Sebastes,* 0.25 lb. for *Merluccius,* 1 lb. for each of the pleuronectids, and 6 lb. for *Urophycis tenuis,* as derived from examination of the catches, and perhaps 1 lb. for the odd fishes of other species, we arrive at a general average weight of some 576 lb. per standard haul, for a water layer perhaps two meters in thickness. This corresponds to 55 lb. of fish and shrimps, above each acre, on the assumption that the breadth of the strip fished by the 82-foot trawl was about 52 feet, and that the distance covered averaged 1.5 sea miles per haul.

We should emphasize that if the foregoing assumptions even approximate the truth, the resultant weight is minimal, because it is based on the further assumption that our nets, in their passage, would capture every individual shrimp, and every fish of appropriate size that lay in their paths. We may well leave this discussion at this point, because no definite information is available as to what proportion of the more active fishes would be likely to dodge the trawls, or to what extent this potential loss would be counterbalanced by the opposing tendency for the lead-ropes to the otter boards to turn inwards, toward the mouth of the net, such other fishes as might be to either side of the latter.[3]

---

[2] Crediting the *Glyptocephalus* and *Hippoglossoides* with an average weight of 1 lb. each.

[3] For discussion of the relative efficiency of trawls rigged in this way—the so-called "V.D." system—as compared with those with the boards close in to the net itself, see Hickling, 1931.

Summary

Findings from 22 trawl-hauls, at 20 stations on mud bottoms in the western and northern parts of the Gulf of Maine, in depths between 120 and 228 meters, August, 1936, are:

1. The faunal community of the water just above these deep mud bottoms is so monotonous that the catch consisted, in every case, almost wholly of five species of fish (*Sebastes marinus, Merluccius bilinearis, Urophycis tenuis, Hippoglossoides platessoides, Glyptocephalus cynoglossus*) and of the shrimp, *Pandalus borealis,* in varying combinations of relative abundance. The only exception was at one station where a larger catch was made of crabs (*Geryon*) than of shrimp.

2. The only other fishes taken were odd examples of the 19 species listed on page 309. The total number of species to be expected in such situations (except as accidental strays) is probably not more than 35.

3. As the nets were arranged to fish off bottom, benthonic invertebrates were not sampled.

4. The most significant faunal contrast, from the regional standpoint, is that *Pandalus* has a well-marked center of population, at least in summer, in the deep bowl west of Jeffrey's Ledge where bottom currents are weak. A positive correlation was also shown between the amounts of shrimps caught at different stations and the percentage of organic matter in the mud, corroborating Hjort and Ruud's (1938) earlier conclusion that *Pandalus* is abundant only where the supply of organic debris on the bottom is relatively large.

5. *Merluccius* was also most plentiful in this bowl, probably in pursuit of shrimp. But the catches do not support any prevailing contrast between this locality and the open basin of the Gulf, in the abundance of any one of the other four fishes of which large catches were made. Neither is any regional contrast suggested in the qualitative composition of the fish fauna over mud bottoms in different parts of the Gulf at the depths in question.

6. The stock of *Merluccius,* in the localities and depths studied, was strongly dominated by the yearlings, an age group the habitat of which in the Gulf of Maine was previously unknown, though the older fish are extremely plentiful there in shoaler water. But the catches of *Sebastes,* of *Hippoglossoides,* of *Glyptocephalus,* and of *Urophycis tenuis* consisted chiefly, or (in the last case) wholly of fish of two years and upwards. The few cod that have been taken in the bowl from time to time have all been very large, though smaller cod as well find their way down into the deeps of the open basin of the Gulf.

7. Length-frequency distribution of the catches added to previous information, indicates that *Sebastes,* in the Gulf of Maine, attains an average length of about 7.5 cm. at one year of age and of about 18 cm.

at two years. But subsequent growth is so slow that age-analysis of larger sizes would require a larger series of measurements than are yet available. Yearlings of *Merluccius* average about 17 cm. by late summer in the deep waters of the Gulf, the two-year-olds about 25 cm.

8. It is estimated that the combined weight of shrimp and fish of all species, in the bowl west of Jeffrey's Ledge, at depths greater than 150 meters, would have averaged at least 576 lb. per haul of 1.5 sea miles with an 82-foot trawl, or 55 lb. per acre of bottom, had the 6-inch stratum next the sea floor been included.

BIBLIOGRAPHY

Bigelow, Henry B., 1927. Physical oceanography of the Gulf of Maine. *Bull. U. S. Bur. Fish.* **40** (Part II) : 511–1027, 207 text figs.

Bigelow, Henry B., and William C. Schroeder, 1936. Supplemental notes on fishes of the Gulf of Maine. *Bull. U. S. Bur. Fish.,* **48** : 319–343.

Bigelow, Henry B., and William W. Welsh, 1925. Fishes of the Gulf of Maine. *Bull. U. S. Bur. Fish.,* **40** (Part I) : 1–567, 273 text figs.

Birdseye, Clarence, 1928. Shrimp Fishin Out o' Gloucester. The Story of a New Industry. *Fishing Gazette,* **45** (No. 4, April 1928) : 12–13, 3 text figs.

Broch, Hjalmar, 1935. Die Bedeutung der Drøbak-Schwelle für die Bodenfauna der Garnelen-Felder. *Avhandl. Det Norske Vid.-Aakad. Oslo,* I. Mat.-Nat. Kl. 1935, No. 5, pp. 1–32.

Goode, George Brown and Tarleton H. Bean, 1896. Oceanic ichthyology. A treatise on the deep-sea and pelagic fishes of the world based chiefly upon the collections made by the steamers "Blake," "Albatross," and "Fish Hawk" in the northwestern Atlantic, with an atlas containing 417 figures. *Mem. M. C. Z.,* Vol. XXII, pp. I–XXXV, 1–553. Also, as *Smithsonian Contributions to Knowledge,* Vol. XXX, (1895) 1896, and as Special Bulletin No. 2, *U. S. Nat. Mus.,* 1895 (issued June, 1896).

Hickling, C. F., 1931. A comparison of the Vigneron-Dahl trawling gear with the steam otter trawl, in the hake fishery. *Cons. Int. Perm. Explor. de la Mer, Jour. du Conseil,* **6** (No. 3) : 421–431.

Hjort, Johan and Johan T. Ruud, 1938. Deep-sea prawn fisheries and their problems. *Hvalrådets Skrifter, Norske Videnskaps-Akademi i Oslo,* No. 17, pp. 1–144, 21 text figs.

Molander, Arvid R., 1925. Observations on the witch (Pleuronectes cynoglossus L.) and its growth. *Cons. Int. Perm. Explor. de la Mer, Publ. de Circ.,* No. 85, pp. 1–15, 4 text figs.

Rathbun, Richard, 1883. Notes on the shrimp and prawn fisheries of the United States. *Bull. U. S. Fish Comm.,* **2** (for 1882) : 139–152.

Rathbun, Richard, 1884. Part V. Crustaceans, Worms, Radiates, and Sponges. In Goode, George Brown, 1884, The Fisheries and Fishery Industries of the United States. Section I, Natural History of Useful Aquatic Animals, pp. 759–850.

Waksman, Selman A., 1933. On the distribution of organic matter in the sea-bottom and the chemical nature and origin of marine humus. *Soil Science,* **36** (No. 2) : 125–147.

Waksman, Selman A., and Margaret Hotchkiss, 1938. On the oxidation of organic matter in marine sediments by bacteria. *Jour. of Mar. Research,* **1** (No. 2) : 101–118, text figs. 34–35.

Walford, Lionel A., 1936. Notes on shrimp fishing along the New England coast. *Memorandum, U. S. Bureau of Fisheries,* Ser. I, No. 57, 5 pp., 2 pls.

Wollebaeck, Alf, 1903. Raeker og raekefiske. Aarsberetning vedk. *Norges Fiskerier,* 1903, vol. 2, pp. 167–229, 20 text figs.

Contribution No. 211

Bulletin of the Museum of Comparative Zoölogy
AT HARVARD COLLEGE
Vol. LXXXV, No. 3

STUDIES OF DEEP-SEA ANGLER-FISHES
(*CERATIOIDEA*)

By Talbot Howe Waterman
Member of the Society of Fellows, Harvard University

CAMBRIDGE, MASS., U. S. A.
PRINTED FOR THE MUSEUM
June, 1939

No. 3 — *Studies on Deep-sea Angler-fishes* (CERATIOIDEA)

BY TALBOT HOWE WATERMAN[2]

I. An historical survey of our present state of knowledge

In 1833 a strange and theretofore unknown fish was thrown up on the beach near Godthaab, Greenland, after a severe storm. It was remarkable for its bulky rounded body lacking ventral fins, black skin sparsely set with large spine-bearing plates, and especially for the "frontal tuft" arising from a longitudinal trough on the forehead and terminating in a bunch of filaments. Captain-lieutenant Carl Holböll procured this fish, unfortunately badly damaged by birds and decay, and sent it to Prof. Joh. C. Reinhardt at Copenhagen. The latter in 1837 described the specimen, which was fifty-eight centimeters in length, as adequately as possible under the circumstances and named it *Himantolophus groenlandicus.* Because of the lack of proper material for study, Reinhardt was not explicit in placing his type in any of the known groups of fishes, but his comparison of this new form with Antennarius and Lophius, especially with reference to the "Pandedusk," or fontal tuft, of Himantolophus, which he thought to be the same structure as, but more highly developed than the first dorsal ray on the head of Lophius, indicated that he believed his species to be related to those fish which comprise the Order *Pediculati* (Regan 1912). *Himantolophus groenlandicus* was the first deep-sea angler-fish to be discovered.

Before 1845 the same Captain Holböll who had collected this Himantolophus had obtained from the deep-sea off Greenland two more new "barbugede Tudsefiske" (called bare-bellied by the Danes because ventral fins are lacking in all the known ceratioid pediculates). One of these two was described in 1844 by Prof. H. Kröyer as *Ceratias holbölli,* while the other remained unnoticed, at least in the literature, until Prof. Chr. Lütken rescued it from dusty oblivion and described it as *Oneirodes eschrichtii* in 1871. Today these first specimens are considered members of three distinct families of the Suborder *Ceratioidea.*

After these first ceratioids from high latitudes were discovered, occasionally others were taken, usually only a single specimen, sometimes taken floating helplessly on the surface, as was *Melanocetus*

---

[1] Contribution Number 211. Woods Hole Oceanographic Institution.

[2] I am very much indebted to Dr. H. B. Bigelow, Director of the Woods Hole Oceanographic Institution, for many valuable suggestions made throughout the writing of this paper; it is a pleasure to thank him for his great assistance.

johnsonii Günther with another fish two or three times as long as itself coiled up in its stomach (Regan 1913). It was not, however, until the great oceanographic expeditions of the last fifty years or so that these peculiar fish were taken in any numbers. By far the most notable contributions to our knowledge of the *Ceratioidea* have come from the Danish oceanographic expeditions on the "Dana" under the leadership of Johannes Schmidt. The 1920–22 Expedition took more than three times as many specimens as had probably been caught altogether up to that time and more than doubled the number of known species (Regan 1925a, 1926), and the 1929–30 Voyage-around-the-world again more than doubled the described ceratioids (Regan and Trewavas 1932) bringing the total, including those more recently described by Parr (1934), Schultz (1934), Fraser-Brunner (1935), and Belloc (1938, p. 303–6) to one hundred and sixty-four species.[1]

Since about eight hundred and sixty specimens are recorded in the literature, this would average five specimens per species. The distribution of specimens has not, of course, been so fortunate, for two of the eleven families, twenty of the forty-one genera, and one hundred (or 61%) of the species are known from single specimens only. A mere handful of species are known from a sufficient number of specimens to allow any accurate ideas to be formed on their vertical and geographical distribution, changes in various parts and proportions in different stages of development, variability within the species, and many other such fundamental problems. There thus remains a tremendous amount of further collecting and comparative study of many more specimens before any adequate generalizations may be made concerning the biological relationships of these weird deep-sea fishes.

It was believed from an early date that the ceratioïds were deep-sea fish, "degenerate" relatives of *Lophius piscatorius* L., living on the bottom with habits generally similar to those of this latter form. A species of Lophius common in the Mediterranean was well known to the ancients by such apt names as βάτραχος ἁλιεύς, Rana marina, Rana piscatrix, and the like. From the time of Aristotle vivid accounts were written of how this sly fish would use its frontal filament, or illicium, for attracting prey. The following passage (p. 67) from Oppian's "Halieutica," which was probably written in the reign of Marcus Aurelius (Emperor 161–180 A.D.), is an interesting example.

Most of the Renaissance ichthyologists, Rondelet, Belon, Salvianus and others, have passages describing similar behavior in Lophius. Ulyssi Aldrovandi in his "De Piscibus" (1612, p. 454–70) gives a non-critical but encyclopedic resumé of the earlier accounts of the matter. With the beginning of the "modern" scientific era, soon after the time of these men, such descriptions of the fishing frog's feeding habits were thrown into disrepute as being but entertaining fishermen's tales.

---

[1] *Oneirodes bulbosus* Chapman (Proc. U. S. Nat. Mus., Vol. 86, p. 538, 1939) brings the total up to one hundred and sixty-five.

Hid in the Slime the *Toad* of Form uncouth
(That Fiſh is all one vaſt extended Mouth)
Her tender Body wraps, on Prey intent,
And ſilent there concerts the great Event.

What ſofter Skin, and ſlower Pace deny,
Wiſe Foreſight and ſucceſsful Frauds ſupply
Within her Jaws a fleſhy Fibre lies,
Whoſe Whiteneſs, grateful Scent, and Worm-like Size
Attract the Shoals, and charm their longing Eyes.
She to allure oft ſhakes the tempting Bait;
They eager preſs, and hurry on their Fate.
But as they near approach, with ſubtle Art
The wily *Toad* contracts th' inviting Part;
Till giddy Numbers thus decoy'd ſhe draws
Within the Circle of her widen'd Jaws.
The Fowler thus the feather'd Race deceives,
And ſtrows beneath his Snare the rifled Sheaves.
The buſy Flocks peck up the ſcatter'd Seed,
Nor midſt their Joy the fatal Engine heed;
Till with loud Clap the tilted Cover falls,
And the cloſe Pit the flutt'ring Prey enthralls.

(Translation of Diaper and Jones, Oxford 1722, lines 153ff.)

Much more recently, for example, Goode (1881, p. 469) considered that the dorsal tentacle of *Mancalias uranoscopus* (Murray) was more likely to be a sense organ for the detection of prey rather than an organ to attract it. This idea has had some confirmation from the work of Brauer (1908, S. 103), who found papillae which he considered to be gustatory, since they were well supplied with nerve fibers, on the bait or esca of the frontal filament of Gigantactis. None the less, there would appear to be a considerable amount of truth in the old stories about Rana piscatrix since recent observations of this fish in its natural habitat such as those cited by Bigelow and Welsh (1925, p. 528) and those of Chadwick (1929) and Wilson (1937) on aquarium specimens indicate that a Lophius lying concealed on the bottom indeed often does lure other fish towards its waiting mouth by waving back and forth over its head the first dorsal spine with its terminal tag-like expansion.

This is undoubtedly true also of Antennarius, the frog-fish, another well-known shore water pediculate. Louis L. Mowbray, Esq., Director of the Bermuda Aquarium, has many times over a course of years observed the angling activities of aquarium specimens of this genus (personal communication 1938). When other small fish were placed in its tank, the Antennarius would slowly maneuver into a position near these other fish and begin to "angle." This consisted of moving about the rod-like first spine of the dorsal fin with its fleshy terminal expansion in a characteristic manner which was different in some cases for different kinds of prey. For example, when one kind of fish was in the tank with the Antennarius, it might slowly draw the first dorsal ray through the water in such a way that the "bait" moved back and forth in a sweeping arc, but when another kind of fish was present, it might vibrate the first dorsal ray and thus merely shake the "bait."[1] Any fish which ventured near the Antennarius to investigate the moving "bait" was drawn very quickly into the enormous mouth cavity of the frogfish by a sudden gulp.

Histrio, the closely related Sargassum fish, which has taken up the specialized habitat of floating Sargassum weed, has also been observed many times under similar conditions, but interestingly enough, this fish has never been seen to use its first dorsal ray as a lure for prey but appears rather to depend entirely in obtaining its food on stealth and its inconspicuous appearance, which resembles remarkably that of the Sargassum to which it clings.

Samuel Garman (1899) in his description of the *Pediculati* from the "Albatross" collection of deep-sea fishes introduced two useful terms in referring to the frontal filaments of the fishes in this order. The whole first dorsal ray with its terminal elaboration he called the illicium. This was a Latin word meaning lure or inducement; it was not, however, at all frequently used by known Latin authors, and I have not been able to find it once used or referred to in any biological context earlier than Garman's, although a number of Latin authors used the related verb forms such as that seen in the quotation from Rondelet given below. According to Dr. Thomas Barbour (personal communication 1938), who was at the time a student in Garman's laboratory, Garman himself believed that he was coining a new biological term in illicium. Regan (1912), recognizing its usefulness, used the word again, and since that time it has been generally employed.

---

[1] Wilson (1937, p. 488) similarly describes two comparable types of angling movements in Lophius.

Garman called the terminal elaboration of the first dorsal ray the esca; this was a Latin word meaning bait, which had frequently been employed since classical times in reference to the use to which Lophius allegedly put its frontal filament. Cicero (ca. 45 B.C.) used esca in a description of the fishing frog's feeding habits in his "De Natura Deorum" (Lib. II, No. 125) ". . . ad quas quasi ad escam pisces quum accesserint . . .", and nearly all of the Renaissance natural history writers whom Needham has called the macro-iconographers of the sixteenth century, employed the same word similarly. Rondelet, for example, in his "De Piscibus Marinis" (1554, Lib. XII, Cap. XX) used it in the following passage concerning Lophius: " . . . ante (oculos) propendent appendices duae . . . quibus veluti esca pisces mira solertia allicit et capit quod non solum gravissimo Aristotelis testimonio, sed etiam piscatorum multorum experientia comprobatum est." It would seem obvious that Garman, who was a fine scholar of the old literature, had the term in question from such sources. Esca has not been used in recent ichthyological writings except by Garman, but I feel that the word would be a useful and convenient one to reintroduce.

Thus when Reinhardt (1837) described the illicium of Himantolophus as being the same as, but more highly developed than the fishing filaments of Antennarius and Lophius, he certainly implied its use as a lure. Lütken (1871), however, seems to have been the first to state this directly, and he even suggested that the shape of the esca and its tentacles in Oneirodes might resemble the head of a nereid worm. The fact that some parts of the esca in at least certain of the ceratioids were luminous was first mentioned by Willemoes-Suhm (1876) in his letters from the "Challenger." This luminescence was thought to make the esca effective in the "eternally dark abysses" of the oceans, where it could not otherwise be seen.

Brauer (1908) in the anatomical section of his classic work on the "Valdivia" deep-sea fish made histological studies of the illicium and its terminal light organ in Gigantactis and Dolopichthys (which latter Brauer identified as Oneirodes). The light organ was described as a spherical, hollow, glandular structure located within the swelling of the esca and surrounded by a layer of reflecting cells and a heavy black pigment capsule. The lumen of the gland was filled by small granular bodies which Brauer considered to be secretory granules produced by the gland cells, some of which could be seen in his preparations breaking down and apparently releasing from their cytoplasm similar structures into the cavity of the organ. This lumen opened into a second, more distal cavity which in turn communicated with the exterior by a canal opening on the mid-dorsal line of the swelling of the esca. Because of its general structure and especially because of the presence of the external opening, Brauer believed this organ to be a "Spitzdrüse," that is a gland whose secretions were forcibly ejected. Never the less, he could not find any muscles in the esca which would permit such an active emptying of the gland's lumen. Neither was he able to find any nerve supplying the light organ although, as mentioned above, branches of an illicial nerve were distributed to the apparently sensory papillae of the esca. A fairly good blood supply, on the other hand, was found running to the luminous gland.

Similar terminal glandular organs may be present on other median fin rays of ceratioids such as those described by Brauer in the caruncles of the dorsal fin in Cryptosparas. As was noted by Regan (1926, p. 11) large specimens of this same genus may even have such structures present on the rays of the caudal fin. Luminescence has been observed by several workers to occur in the escal light organ, and Beebe (1934, p. 191–2) observed light coming from swellings on the tips of the first three dorsal rays in a ceratioid seen by him from the bathysphere; whether all such swellings on ceratioid fins are luminous or not is not known.

Dahlgren (1928) without more than merely stating that such was the case, described from histological examination the granules filling the cavity of the escal light organ of a specimen of Ceratias as luminous bacteria. He presumed that these organisms were living symbiotically within the esca, supplying light for the fish's bait in return for nutriment provided by a sort of culture medium maintained within the luminous gland by the activity of the secretory cells. A similar type of symbiosis had previously been described for the light organs of three or four other fishes, in some of which the results were quite convincing since careful bacteriological methods had been employed. (Dahlgren gave several references; see also Yasaki and Haneda 1936).

This same sort of interesting relationship has been found to occur in a number of luminous cephalopods. Bacteriological investigations of the light organs of a considerable number of different kinds of these animals (Kishitani 1932, Herfurth 1936) have shown that only in the case of luminous organs which open to the exterior by a canal or pore were symbiotic luminous bacteria present in large numbers; those light organs which were closed to the sea water did not contain the symbionts. The light organs of all the fish which were believed to cultivate luminous bacteria in their lumina were also open to the exterior. Dahlgren's conclusions concerning the bacterial origin of the light in Ceratias were thus in general agreement with such studies. However, in the case of another fish, the macrurid, *Malacocephalus laevis,* in which the light organ was open to the outside the luminescence was apparently not a bacterial luminescence since microscopic study demonstrated that the granules present in the material filling the lumen of the gland were not bacteria (Hickling 1925). Furthermore, the test for luciferin and luciferase,[1] "substances" known to be involved in the luminescent reaction of a number of different organisms was positive. These materials have never been convincingly detected in bacteria so that it would appear highly unlikely that they were being extracted from symbiotic luminous bacteria in this case. It is clear then that at least two methods of producing light are employed by fishes, and it is possible that combinations of the two may be found in the same animal, but only after many more, careful investigations of the various types of luminous fishes and their light organs will it be possible to draw any satisfactory general conclusions concerning these matters.

Several references in the earlier literature to cases where living ceratioids were examined in the dark, state that the light produced by the escal light organ was apparently under "voluntary" control; this meant at least that the luminescence was not continuous. In 1936 I had the opportunity to observe a living Dolopichthys which was taken by the research ship "Atlantis" in the Sargasso Sea. Still feebly moving this specimen was quickly removed from the net and placed in cold water. In the ship's dark-room, I was able to observe the luminescence of the escal light organ during the ten minutes or so that the fish remained alive. This remained dark until the fish was quite actively stimulated mechanically. When it did luminesce, the light was confined within the esca, which was transparent and more or less free from pigment distally, and no trace of luminous secretion was observed to be extruded from the external pore of the organ. The light was bluish green in color like that of the majority of luminous organisms and lasted for five or six seconds beginning dimly and rising to a peak in a second or so, maintaining the maximum intensity for several seconds, and then slowly fading out.

---

[1] See E. N. Harvey. 1935. Luciferase, the enzyme concerned in luminescence of living organisms. Ergeb. Enzymforsch. Bd. IV, S. 365-79.

If the luminescence of ceratioids is a bacterial luminescence, the question of the control of the light is a very interesting one, for luminous bacteria under normal conditions luminesce continuously, unlike all animals which produce their own light. A simple method of control of the light of these symbiotic bacteria would be through the amount of oxygen available to the bacteria, which luminesce only under aerobic conditions. It is bacteriologically conceivable that anaerobic conditions could be easily developed within the lumen of the light organ which would, when they became completely anaerobic, extinguish the light entirely. Sufficient oxygen for luminescence (the amount necessary is extremely small as was shown, for example, by the experiment of Beijerinck (1902) in which sufficient oxygen for momentary luminescence of the previously dark bacteria was obtained in a suspension of clover leaves illuminated by the light of a single match) could easily be supplied by a blood system such a Brauer (1908) described in the ceratioids he studied. The present very imperfect state of our knowledge of the physiology of bioluminescence makes it unwise to do more than outline a few of the more salient points in this connection. Certainly the problem of the control of luminescence in animals is one of the least understood, yet biologically one of the most interesting of the many aspects of bioluminescence.

The nineteenth century students of ceratioids believed that these fish were benthonic, like Lophius. Filhol (1885, p. 81) even has an imaginative picture of *Melanocetus johnsonii* Günther in which several specimens are shown buried up to their eyes in the mud with their illicia waving over their heads. The fact that the mouth in this species opens upwards at a sharp angle made it a bit difficult to make these fish look plausible buried tail-downward in the ooze of the ocean bottom. Garman (1899) in his discussion of the genotype of Dolopichthys remarked on the improbability of such fish being active swimmers and stated his belief that their peculiar body form, fin reduction, and smooth skin were adaptations for life in the soft muds of the sea floor. It was Brauer (1906) who first showed that the ceratioids were bathypelagic rather than benthonic forms. He based his demonstration mainly on the analysis of vertical closing net hauls made by the "Valdivia" and which showed at what depths in the water the specimens were fished; he furthermore pointed out that several ceratioids which had been taken previously had been found with scopeline and other non-benthonic fish in their stomachs. It is generally believed today that, with the exception of the young, which have often been taken in shallower water, the deep-sea angler-fishes live bathypelagically largely at depths ranging from 500–5,000 meters (Regan and Trewavas 1932, p. 12; Beebe 1937, p. 207).

The occurrence of dwarf males living attached to the relatively gigantic females which has been described in a number of deep-sea angler-fish is such a striking and bizarre phenomenon that it has become a part of everyday scientific knowledge. Nevertheless, no thoroughly satisfactory analysis of the few available facts concerning this interesting sexual relationship of the ceratioids has as yet been published. Regan and Trewavas (1932) give a good descriptive section on sexual dimorphism, however.

Saemundsson (1922) was the first to discover the attached males. He noticed two small fish grown fast to the belly of a large female *Ceratias holbölli;* he did not recognize them as dwarf males but thought that they might possibly be young of the same species since they showed certain well marked similarities to the larger fish. Three years later Regan (1925b) from a dissection of another specimen of *C. holbölli* to which a small fish was attached showed that this latter was a male with a fairly well developed testis and that the larger fish was a female.

Up to the present time fourteen specimens of these dwarf males have been discovered attached to twelve (out of the approximately five hundred and fifty known) female ceratioids. Most of these females had only one male grown onto them, but Saemundsson's specimen as mentioned above, had two, and one female of *Edriolychnus schmidti* (Regan and Trewavas 1932, plate IX, fig 2) had three of them. The males have been found attached head-on to the females by outgrowths from either the lower jaws or from both the upper and lower jaws to a papilla raised up on the surface of the body of the females. The place of attachment was apparently random since males have been found fastened to the belly, head, and even the preopercular spine of the females.

The female angler-fish so far found with attached males belong to four distinct families of the Sub-order *Ceratioidea.* Regan (1925, p. 397) at first believed that attached males were characteristic of the whole sub-order; this point of view was also favored by Parr. The latter worker, however, (1930) after a study of the anatomy of the then rather anomalous family of ceratioids, the *Aceratiidae*, was led to conclude that these small fish, lacking an illicium externally at least (except for Anomalophryne Beebe, 1929) and generally possessing pincer-like rostral denticles, large nostrils and olfactory organs, were free-living stages of male ceratioids theretofore recognized only in the attached forms. A careful study of the viscera of one of these free-living non-illiciate fishes, *Rhynchoceratias longipinnis*, was made by Parr (1930). This specimen was indeed a male and had a testis apparently as large relatively as any found in the attached males which have been investigated in this respect. Determination of the sex of as many of the aceratiids as possible has led to the discovery that they were all males; furthermore, similar study has shown all the illiciate "typical" ceratioids to be females. From anatomical evidence it has been possible in most cases to assign the free-living males to families previously known only from females. Free-living males then have been found to occur in five of the eleven families of the *Ceratioidea*.

Parr (1930, 1932) suggested that the free-swimming males were doubtless merely at an earlier stage in their life history than were the attached males and would consequently become attached at some later time. On the other hand, Regan and Trewavas (1932, p. 20) thought it probable in view of Parr's discovery of the free-living males, that attached males occur only in the four families in which they had been found up to that time and that all the other families of ceratioids had free-living males. This point of view was not sustained by any direct evidence presented but seemed rather to rest on Regan's (1925b, p. 396) assumption which he had maintained from the beginning that the attached males became fastened to the females at an early stage, probably shortly after the larval stage, certainly before the gonads have matured.

Evidence for a long period of attachment at least was found (Regan and Trewavas 1932, p. 42) in the skull of an attached male *Ceratias holbölli* in which certain osteological peculiarities were believed to have resulted from the male's having been much smaller at the time of attachment. However, if Regan's original assumption corresponds to the facts then no free-living males with as well developed testes as Rhynchoceratias could be found in a family which had parasitic males. Yet free-living males have been found in the *Linophrynidae*. Thus the situation becomes rather confusing in the paragraphs concerning the male linophrynids (Regan and Trewavas 1932, p. 15ff) since both free-living and attached males are described in this family. The free-swimming males of the type of Aceratias were shown to be very similar to the attached males of the Genus Borophryne. In spite of the fact that the free-living male *Linophrynidae* listed by Regan and Trewavas (1932) average over twenty-five percent longer in standard length than the attached males discussed, these authors felt obliged to maintain without qualification the assumption of an early time of attachment and the double hypothesis that free-living males occur in certain families of ceratioids and attached ones occur only in the remaining families. These views would seem to be rather troublesome to maintain especially since Parr's (1934, p. 56ff) discovery of a free swimming male, *Borophryne masculina*, belonging to a genus in which two females with attached males are already known. In this case, too, the free-living male is somewhat larger than the attached ones of the same genus.

It would thus seem clear that the simplest reasonable explanation of the facts would be that free-living and attached males might well be found to occur in all of the deep-sea angler-fish which have developed a marked sexual dimorphism. Furthermore, as Parr has pointed out (1930, p. 134), the males do not generally become attached at an early stage of their development since, for example, amongst the *Linophrynidae* mentioned above there are one hundred and thirty free-living males recorded in the literature and only eight attached males. The time of attachment and consequently the period during which this union of male and female lasts would appear from the evidence reviewed to vary with the individual circumstances.

It has been generally assumed that the development of males which were first free-swimming fairly active fishes and then sessile on the females was an adaptation to the fact that the female ceratioids were solitary sluggish animals whose chances of mating in the dark abysses of the oceans would be rather negligible if the males of the group were of similar habit. This adaptational point of view would go on to suggest that if a male and a female of the same species were so fortunate as to find one another, some means of their continued association until their reproductive functions had been discharged would be of great advantage. Thus it may be that certain of the individual males find and attach on to their mates soon after the post-larval period, whereas others swim about seeking mates until they have become mature, and doubtless still other males never do find a female of their species. Also it may be in the more primitive families of the sub-order, in which no attached males have yet been found, that instead of actually growing fast to the females, as was the case of the attached males already known, the males merely nip on to the females for a relatively short period. The fact that only two percent of all the known female ceratioids and only seven percent of the females of just the families in which attached males have already described have males attached to them may be indicative of a relatively brief period of union between the two sexes. On the other hand, it may rather indicate, in conjunction with the very small size of the great majority of the angler-fish which have yet been captured, that only a relatively few mature fish have been taken so far.

Another point of interest concerning the male ceratioids is that although fifty-seven percent as many free-living male specimens as females have been found, there are only twenty percent as many species of males as there are female species. Thus there are not nearly enough species of males to pair them up with the females. If all the specimens which are assumed to be female are, it would seem likely then that either differences which were either individual or ontogenetic have been used in defining many of the female species, or else the ability to differentiate between males of different species has not been sufficiently developed to distinguish the rather obscure details which separate them.

The fact that both the *Melanocetidae* and the *Himantolophidae,* the most primitive familes of the *Ceratioidea,* have two genera of males to one of females has been pointed out by Regan and Trewavas (1932, p. 21) to be in striking contrast with the rest of the sub-order. The fish in one of the male genera in both cases, Centrocetus and Lipactis, were more like females in shape than any other known free-living males; teeth in the jaws, which were generally absent in male ceratioids, were present, and the rostral denticles were not well developed. The more typically ceratioid appearance and the very small size of these peculiar males would suggest the possibility that they were merely juvenile specimens. A minute male of the Family *Diceratiidae, Caranactis pumilus,* would presumably belong in the same category.

The physiological significance of the attachment of the males to the females in the deep-sea angler-fish is a point of great interest. Regan from his first paper on the subject has maintained that the attached males were nutritional parasites on the females. Sections cut through the region of attachment of the two fish were believed to demonstrate a complete blending of the vascular systems in that region indicating that they were continuous from one fish to the other (Regan 1926, p. 12). Furthermore, the mouth of the males, because of the nature of the attachment to the female, was no longer available for active feeding, the stomach and gut were remarkably degenerate, and the union between the two was believed to last for a long time. All of these conditions would seem to indicate that the males must depend on some unusual source of nourishment. Further descriptions and figures of the region of fusion between the male and female, as it appeared in serial sections, were given by Regan and Trewavas (1932, p. 21); sinuses of the region were traced out as connecting the blood vessels of the pair through a capillary network on each side, thus proving the direct continuity of the blood streams that had been strongly suggested by previous studies. Parr (1930, 1932), however, expressed the opinion that the nutritional aspects of the continuity of the circulatory systems might not be as important as previously believed. He was led to this point of view, among other things, by the relatively enormous size of the liver in the specimen of free-living male whose anatomy he had investigated. Thus before the time of its attachment to the female, the male might store up a large quantity of food in its liver, which would be an efficient storage space; this food could then be used by the male during the period of his union with the female. Evidence in support of this suggestion may be obtained from a number of figures in Regan and Trewavas (1932, pp. 16, 17, 20, 22) of the visceral anatomy of male ceratioids. These figures show that the free-living males had relatively large livers whereas in the attached males which have been examined the livers were small. It is interesting to note in this connection that the attached male of *Ceratias holbölli* which Regan and Trewavas believed from osteological evidence to have been fastened to the female for a long period had apparently an extremely minute liver since this organ was neither shown in the figure of the anatomy of this fish nor mentioned in the text (Regan 1925b, fig. 4 and p. 392). Perhaps in cases where the attachment of the male lasts over a longer period than could be supplied with food stored in the liver, the nutritional possibilities of a confluence or even placenta-like arrangement of the blood streams may come to be realized.

A further structural arrangement pertinent to these matters has been known from the time of Saemundsson's (1922) discovery of the first attached male. Namely, the fact that in every case although the mouth of the attached fish becomes more or less occluded from the nature of the attachment, lateral openings into the mouth cavity are retained. These are believed to permit the circulation of a respiratory current. Regan (1926, p. 14) stated that since the attached males have a well developed heart and gills, they do not depend on the blood of the females for oxygen but only for nutritive materials. As Parr (personal communication 1938) has pointed out, if arrangements for a respiratory current and normally developed respiratory and circulatory systems are maintained by the attached males, they could not be receiving sufficient oxygenated blood from the females for their own, probably meager, needs. Either then the male receives only venous blood from the female or else not much blood at all. Two facts would appear to cast some light on the probability of the former alternative: First, Regan (1926, p. 14) states that both arteries and veins run into the capillary network of the tissues connecting the males and the females. Second, if the males were carrying the added excretory burden of a considerable venous circulation from the females, unusually large kidneys might be expected in the attached males; these organs have not been found to be of greater size, however, than those found in the free-living males. If these arguments carry any weight, then we are left with the alternative that there is not much blood interchange between the males and the females.

One idea that has been suggested by both Regan and Parr is the possibility that the continuity of the blood streams would permit an hormonal interchange between the male and the female which might affect the differentiation of the gonads, and synchronize their maturation and the discharge of their sexual products. However, from the general results of vertebrate endocrinology, especially as related to parabiosis, it would appear unlikely that the attachment of the males, provided they were sexually differentiated (and there is no mention in the literature of any attached "male" in which the gonad could not be easily identified as testis) and normal as to their endocrine functions, was of any particular significance (Hisaw, personal communication 1938). It must be admitted, never the less, that in animals which have become morphologically as highly specialized as the ceratioids it would be difficult to predict with any degree of assurance what special physiological functions they may have developed in the course of their evolution.

The foregoing account has attempted to outline and assay the facts which are known concerning the deep-sea angler-fish. In the analysis of even the most recent knowledge of these fish the discussion has been filled with probabilities, suggestions, ideas, possibilities, and the like, and nearly every problem approached was found to rest in a highly unsettled and hypothetical state. This at the present time is true of our biological knowledge of all bathypelagic organisms. The great difficulty and expense of obtaining material and the well nigh insuperable barriers to experimental work in this field have been the principal deterrents to great advances in these directions. It is to be hoped, however, that in the future with the further coöperation of the great oceanographic institutions and their research vessels that many of these intriguing and significant problems may be satisfactorily solved and fitted into the general body of physical and biological knowledge which constitutes the science of oceanography.

BIBLIOGRAPHY

Beebe, W.

1929. *Haplophryne hudsonius.* A new species; description and osteology. Zoölogica, Vol. 12, p. 21–36.

1934. Three new deep-sea fish seen from the bathysphere. Bull. N. Y. Zoöl. Soc., Vol. 37, No. 6, p. 190–3.

1937. Preliminary list of Bermuda deep-sea fish. Zoölogica, Vol. 22, p. 197–208.

Beijerinck, M. W.

1902. Photobacteria as a reactive in the investigation of the chlorophyll function. Proc. Roy. Acad. Amsterdam, Vol. 4, p. 45–9

Belloc, G.

1938. Liste des poissons pélagiques et bathypélagiques capturés au cours de la cinquième croisière avec diagnoses préliminaires de deux espèces nouvelles. Rev. Trav. Office des Pêches, T. XI, fasc. 3, p. 281–313.

Bigelow, H. B. and W. W. Welsh

1925. Fishes of the Gulf of Maine. Bull. U. S. Bur. Fisheries, Vol. 40 (1924), Pt. 1, p. 1–567.

Brauer, A.

1906, 1908. Die Tiefsee-Fische. Lief. I, Systematischer Teil, S. 1–420. Lief. II, Anatomischer Teil, S. 1–266. Wiss. Ergeb. Deut. Tiefsee-Exped. . . . "Valdivia," Bd. 15.

Chadwick, H. C.

1929. Feeding Habits of the Angler-fish, *Lophius piscatorius.* Nature, Vol. 124, p. 337.

Dahlgren, U.

1928. The bacterial light organ of Ceratias. Science, N. S., Vol. 68, p. 65–6.

Filhol, H.

1885. La vie au fond des mers. Paris.

Fraser-Brunner, A.

1935. New or rare fishes from the Irish Atlantic slope. Proc. Roy. Irish Acad., Vol. 42B, p. 319–26.

GARMAN, S.

1899. Reports on an exploration . . . by the "Albatross" during 1891. XXVI, The Fishes. Memoirs Mus. Comp. Zoöl., Vol. 24, p. 1–431.

GOODE, G. B.

1881. Fishes from the deep water on the south coast of New England obtained by the U. S. Fish Commission in the summer of 1880. Proc. U. S. Nat. Mus., Vol. 3 (1880), p. 467–86.

HERFURTH, A. H.

1936. Beiträge zur Kenntnis der Bakteriensymbiose der Cephalopoden. Zeit. Morph. Ökol. Tiere, Bd. 31, S. 561–607.

HICKLING, C. F.

1925. A new type of luminescence in fishes. J. Mar. Biol. Assoc., N. S., Vol. 13, p. 914–37.

KISHITANI, T.

1932. Studien über Leuchtsymbiose von japanischen Sepien. Fol. Anat. Jap., Bd. 10, S. 315–418.

KRÖYER, H.

1844. Meddeler Forögelser til Kundskab om de grönlandske Fiskearter. Overs. K. D. Vidensk. Selsk. Forh. 1844, No. 8, S. 138–41. (Probably published before the following; *Ceratias holbölli* here nomen nudum.)

1844. *Ceratias Holbölli* Kr. Naturh. Tidsskr. Bd. 1, Ser. 2, S. 639–49.

LÜTKEN, C.

1871. *Oneirodes Eschrichtii* Ltk. en ny grönlansk Tudsefisk. Overs. K. D. Vidensk. Selsk. Forh. 1871, S. 56–73. (An English translation of this paper appeared in Ann. Mag. Nat. Hist., Ser. 4, Vol. 9, p. 329–44, 1872).

PARR, A. E.

1930. On the probable identity, life-history, and anatomy of free-living and attached males of the ceratioid fishes. Copeia, 1930, p. 129–35.

1932. On a deep-sea devilfish from New England waters and the peculiar life and looks of its kind. Bull. Boston Soc. Nat. Hist., No. 63, p. 3–16.

1934. Report on experimental use of a triangular trawl for bathypelagic collecting. Bull. Bingham Oceanogr. Coll., Vol. 4, Art. 6, p. 1–59.

REGAN, C. T.

1912. Classification of the teleostean fishes of the Order *Pediculati*. Ann. Mag. Nat. Hist., Ser. 8, Vol. 9, p. 277–89.

1913. A deep-sea angler-fish, *Melanocetus johnsonii*. Proc. Zoöl. Soc., London, 1913, p. 1096–7.

1925a. New ceratioid fishes from the North Atlantic, the Caribbean Sea, and the Gulf of Panama, collected by the "Dana." Ann. Mag. Nat. Hist., Ser. 9, Vol. 15, p. 561–7.

1925b. Dwarfed males parasitic on the females in oceanic angler-fishes (*Pediculati Ceratioidea*). Proc. Roy. Soc. Lond., Vol. B97, p. 386–400.

1926. The pediculate fishes of the Suborder *Ceratioidea*. Danish "Dana" Exped. 1920–22, Rep. No. 2, p. 1–45.

Regan, C. T. and E. Trewavas

1932. Deep-sea angler-fishes (*Ceratioidea*). Carlsberg Foundation "Dana" Report No. 2, 1932, p. 1-113.

Reinhardt, J. C.

1837. Ichthyologiske Bidrag til den Grönlandske Fauna. K. Danske Vidensk. Selsk. Nat. og Math. Afh., 4te Raekke, Bd. 7, S. 83–196.

Saemundsson, B.

1922. Zoölogiske Meddelelser fra Island, XIV. 11 Fiske, ny for Island, og supplorende Oplysninger om andre, tidligere kendte. Vidensk. Medd. Köbenhaven, Bd. 74, S. 159–201.

Schultz, L. P.

1934. A new ceratiid fish from the Gulf of Alaska. Copeia, 1934, p. 66–8.

Willemoes-Suhm, R. von

1876. Challenger Briefe an C. Th. E. von Siebold. Zeit. Wiss. Zoöl., Bd. 26, S. lxxxi.

Wilson, D. P.

1937. The habits of the Angler-fish, *Lophius piscatorius* L., in the Plymouth Aquarium. J. Mar. Biol. Assoc., N. S., Vol. 21, p. 477–96.

Yasaki, Y. und Haneda

1936. Über einen neuen Typus von Leuchtorgan im Fische. Proc. Imp. Acad. Tokyo, Vol. 12, p. 55–7.

II. Three new species

In the course of examining hauls made from the research ship "Atlantis" during the summers of 1936 and 1937 a few small *Ceratioidea* were found. Three of these are apparently new species belonging to 3 distinct families of this suborder: *Gigantactinidae, Linophrynidae,* and *Oneirodidae.*

GIGANTACTIS LONGICIRRA, spec. nov. (Figs. 1 and 2)

1 specimen: holotype, M C. Z. No. 35,065.

Total length about 62 mm., standard length 39 mm. Illicium terminal on snout, length from articulation with basal bone to distal end of the bulb 15 mm. (39% of S. L.). Length of lower jaw 7 mm. (18% S. L.); eye diameter 0.8 mm. (2% S. L.).

Fin rays. D.8, A.6, C.8, P.18. Branchiostegal rays 6 (2+4); pectoral radials (pterygials) 5 (4+1).

Dentition. All teeth curved and depressable inward or backward. Lower jaw: 13–14 teeth on each side, of different sizes, ranged in 2 rows one within the other. Upper jaw: 8 in a single row on each premaxillary; maxillary toothless. Lower pharyngeals toothless; upper pharyngeals: 2nd and 3rd pharyngobranchials each have 3–4 large teeth. Palatines and vomer toothless.

The esca[1] (Fig. 2) consists of a somewhat pear-shaped swelling, rounded and blunt distally, and bearing at its proximal end 20 slender filaments which are 60–300% as long as the swelling itself. Each of these filaments terminates distally with a just perceptible bulbous expansion. Within the pear-shaped swelling is a heávily pigmented spherical core (the light organ) with a hemispherical prominence of about half its own diameter projecting from it postero-dorsally. The core is borne on the larger end of a conical expansion of the inner stalk which runs up the center of the illicial stem.

The nostrils are tubular; lateral line organs on projecting tags or flaps of pigmented skin are present on the head, body, and also the rays of the caudal fin. There are no channels or grooves connecting these organs with one another. The skin is closely set with small subcircular plates each bearing a short sharp spine.

No pelvic bones were found in a dissection of one side of the specimen.

---

[1] For definition and origin of this term and "illicium" see preceding section, p. 68–9.

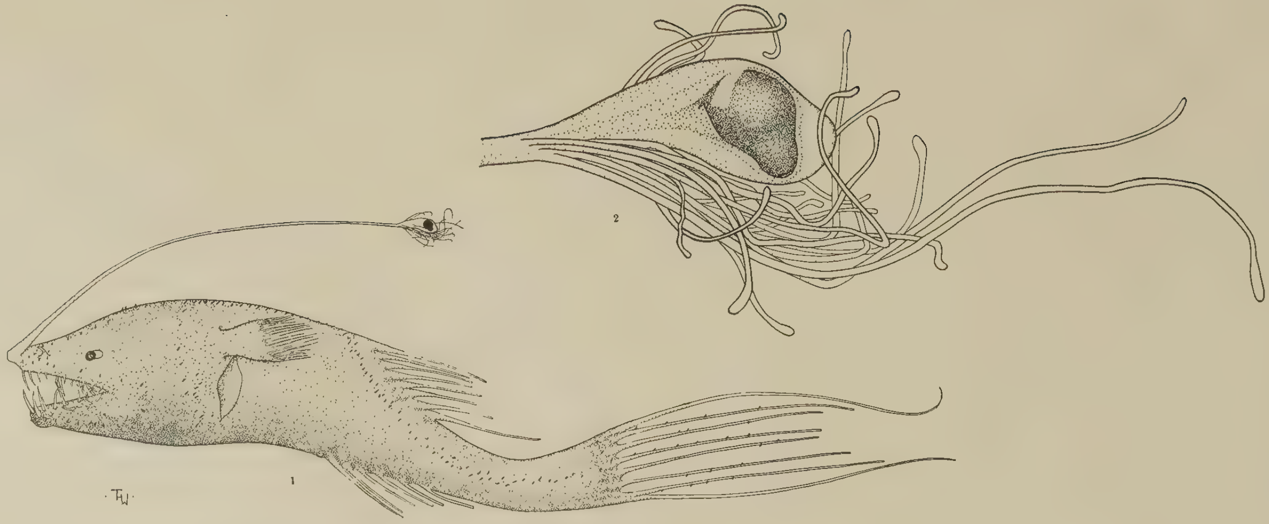


Fig. 1. *Gigantactis longicirra*, spec. nov. Standard length 39mm.
Fig. 2. Lateral view of esca of *Gigantactis longicirra*, spec. nov.

Color. Chocolate brown (after fixation in formalin, followed by alcohol.)

Type locality. "Atlantis" Station 2894, July 20th, 1937, continental slope about 300 miles east of Cape May, New Jersey (39°06′N., 70° 16′W.), closing net at 1000 m., 4 A.M., depth to bottom 2860 m.

Discussion

Clearly the slender, elongate body of this ceratioid, the attenuate frontal region of its skull, and the long illicium located terminally on the snout demonstrate that it belongs to the *Gigantactinidae* Boulenger, 1904, and more specifically to the genus Gigantactis Brauer, 1902. Of the 8 individual specimens of the genus, which have been taken previously, 7 are types of as many different species (Brauer, 1902; Regan, 1925, 1926; Regan and Trewavas, 1932; and Fraser-Brunner, 1935) from all of which the present specimen is notably distinct. Four characters clearly set it apart from any other known form. These are:

1. The number of dorsal rays is greater by 2 than that given for any of the other *Gigantactinidae;* all other members of the present genus have 6 and *Rhynchactis leptonema* 3 (Regan, 1925)[1].

2. In the pectoral appendage one more pectoral radial bone is present than has been described for any of the other *Pediculati,* which primitively have only 3 of these bones (Gregory and Conrad, 1936, p. 202). Regan and Trewavas (1932) have found 4 of these elongate basalia in both *G. sexfilis* and *Rhynchactis leptonema* and suggested (p. 25) that the presence of 4 of them is a diagnostic feature for the *Gigantactinidae.*

3. The length of the illicium from its proximal end, where it articulates with the modified pterygiophore or "basal bone," to the distal end of the bulb of the esca is less than 40% (38%) of the standard length. In previously known species, including smaller as well as larger specimens, this measure was always 60% or more of the standard length, varying from 60% in *G. exodon* (where it might be a juvenile character since the type is only 25 mm. in standard length) to 400% in *G. macronema.*

4. The esca is notably different from that described for any other ceratioid. Except for *exodon,* all other gigantactids have terminal filaments present on the esca whereas in the present fish there is no

---

[1] Only 5 dorsal rays are shown in the figure of *G. vanhoeffeni* although 6 is the number given in the description (Brauer, 1906).

trace of such. In *exodon*, however, the swelling of the esca tapers distally; this is definitely not the case with the new species. Yet in the only other species of Gigantactis, *ovifer* and *filibulbosus*, in which the bulb does not taper distally there are two terminal filaments present in the esca and no proximal filaments at all. The proximal filaments of the new species' esca are more numerous and longer proportionately than any such filaments found in other specimens of Gigantactis.

A further point of interest in *G. longicirra* concerns the lateral line organs. In other members of the family (Regan and Trewavas, 1932, p. 24) these occur on "stalks" rather than on "tags" as found in *longicirra*. If this difference does not depend on confusion of terminology it may well be a fifth clear distinction of the present species. Brauer (1906) figures *G. vanhoeffeni* with lateral line organs on the caudal rays much as in *longicirra* but does not mention this unusual phenomenon in the text.

Although the standard length of the present specimen is only 40% of that of the largest specimen of Gigantactis yet taken (the type of *G. macronema* Regan, 1925), one half of the types of previously known gigantactinids are smaller. Thus it would appear that the characters used to distinguish *G. longicirra* are no more likely to be juvenile than are those for half the members of the genus. Furthermore, it would not seem likely that the structural characteristics listed above (at least the first two) had been derived by growth or simplification as a stage in the life history of some previously known form. However, in the absence of any direct evidence concerning the changes which take place in Gigantactis in the course of its ontogeny, it is rather difficult to make any predictions concerning such aberrant forms.[1]

LINOPHRYNE ALGIBARBATA, spec. nov. (Figs. 3 and 4)

1 specimen; holotype, M. C. Z. No. 35,066.

Total length 40 mm., standard length 28 mm. Illicium suprarostral, length from articulation with basal bone to distal end of bulb 7 mm. (25% of S. L.), basal bone not exserted in present condition of specimen.[2] Bulb of esca 50% of length of illicial stem. Length of lower

---

[1] But see Fraser-Brunner's (1935) suggestion that the presence of teeth on the lower jaw well down on the sides of the chin and away from the bite of the jaws was a juvenile character in Gigantactis.

[2] Since the basal bone (modified pterygiophore) of the illicium is freely moveable and supplied among others with extensor and retractor muscles, the amount of its exsertion in any specimen depends on the condition of these muscles on fixation. Clearly, however, certain forms such as Mancalias and Lasiognathus must always have a considerable portion of the basal bone exserted whereas others as Edriolychnus and Himantolophus do not.

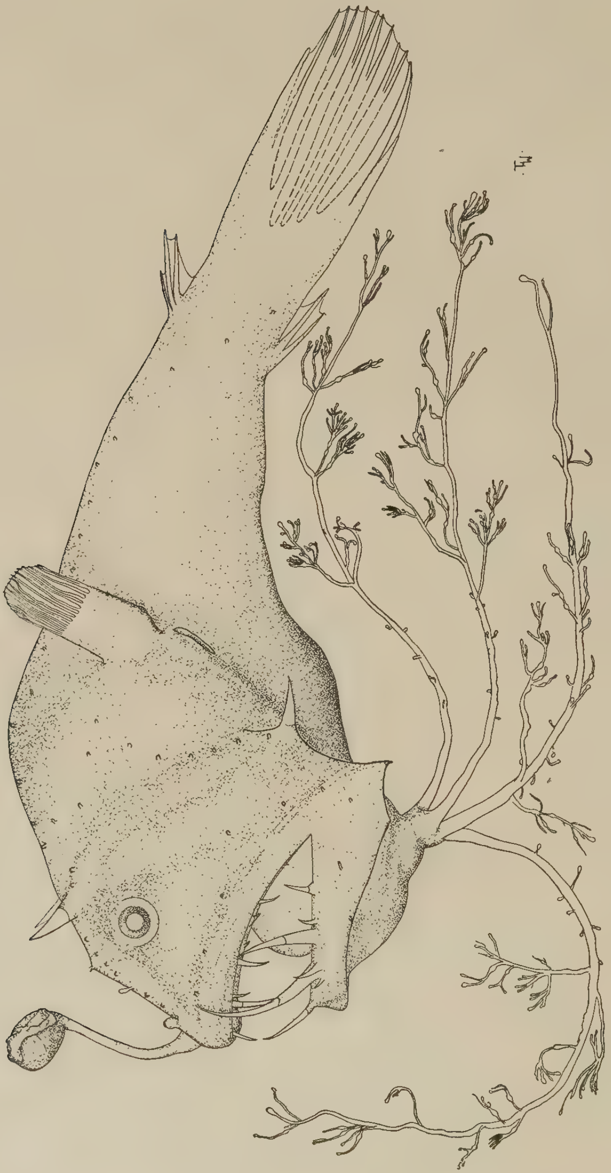


Fig. 3. *Linophryne algibarbata*, spec. nov. Standard length 28mm.

jaw to articular spine 9 mm. (31% S. L.). Barbel length about 24 mm. (86% S. L.).

Sphenotic and preopercular spines large and sharp, free of skin except at their bases, smaller frontal and articular spines present.

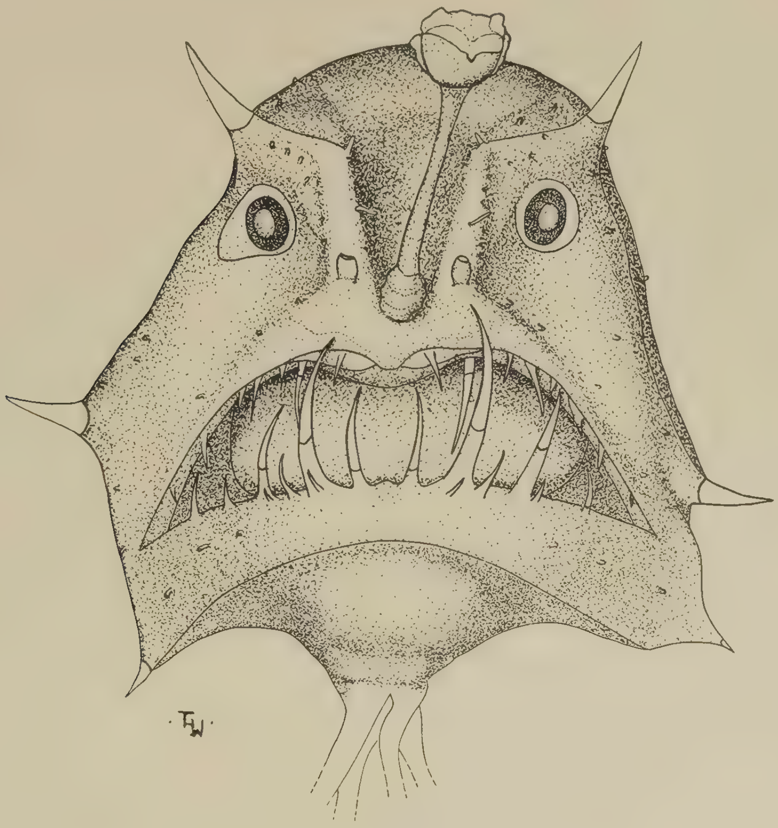


Fig. 4. *Linophryne algibarbata*, spec. nov.

Dentition. Teeth depressable inwards. Lower jaw: 7–8 irregularly arranged teeth including 1 very large (15% S. L.) and 2 smaller fangs on each side. Upper jaw: 7–8 irregularly arranged teeth including 1 large fang on each premaxillary; maxillary toothless. Large fangs saber-like, sheathed proximally in pigmented epithelium. Lower pharyngeals toothless, 3 teeth each on second and third upper pharyngeals (pharyngobranchials). Palatines toothless; 2 teeth on vomer.

Fin rays. D.3, A.2, P.16. Brachiostegal rays 4 (1+3); pectoral radials (pterygials) 3 (2+1). Pigmented skin runs out over all fin rays.

Barbel arises from short stalk which divides immediately into four main branches of approximately equal length and diameter; each of these gives rise to irregularly arranged, much shorter secondary and tertiary branches, which in most cases have knob-like swellings along their lengths and terminally.

Esca consists of a subspherical bulb bearing around its anterodorsal surface a roughly horse-shore shaped ridge which consists of a median and two lateral lobes. In the median line, just posterior to this ridge is a low silvery papilla behind which is the external pore of the luminous organ of the esca. A slight longitudinal ridge of short extent is present immediately posterior to this. A black pigment cup which is visible through the transparent outer layers of the bulb surrounds about half of an inner sphere (the light organ), the exposed, distal part of which appears silvery. The rim of this pigmented cup has two distinct notches in it, one anterior, which is visible in Fig. 4, and one posterior.

The nostrils are large and tubular; lateral line organs are present on the head and body; these are situated on tags of pigmented skin, a few of which are notably larger than the rest. No channels or grooves connect these organs.

No pelvic bones were found in a dissection of one side of the specimen.

The skin is smooth and (after fixation in formalin followed by alcohol) chocolate brown in color.

Type locality. 39°06′N., 70°16′W., July 20th, 1937; closing net, 400 m., 5 A.M., depth to bottom 2860 m.

Discussion

In recent papers Regan and Trewavas (1932) and especially Parr (1934) have organized and extended our knowledge of the genus Linophryne. Twenty-five specimens belonging to this genus have been reported in the literature. For the twenty-one of these which are adequately known thirteen species and five subspecies have been defined. Thus nine species and two subspecies are known only from single specimens. In no case has more than one fish of a species in this genus been taken in a single catch.

The characteristics which distinguish *L. algibarbata* most clearly from any of these previously known species are as follows:

1. The absence of either terminal or lateral filaments or of digitiform appendages on the esca. These occur in all other known species in some form or combination.

2. The general pattern and the method of branching of the hyoid barbel. While this appendage is similar in a general way to that of *L. arborifera* and of *L. macrodon,* it differs distinctly from these not only in the fact that the four main branches are of approximately equal length and diameter but also in the details of the secondary and tertiary ramifications.

3. Presence of only 4 branchiostegal rays instead of the 5 which Regan and Trewavas (1932) had concluded from their dissections of *L. racemifera, Halpophryne sp.,* and *Aceratias indicus* were characteristic of the Family *Linophrynidae.* However, the present observation shows that more specimens will have to be investigated before the significance of this point for diagnostic purposes will be apparent.

Since the present specimen differs from forms previously described in the fundamental pattern of the barbel and of the terminal appendages of the esca, it is clear that a new species is necessary here rather than a subspecies, such as those set up in *Linophryne arborifera* and *L. coronata* by Parr (1934) on the basis of minor variations in the details of these structures.

DOLOPICHTHYS ALBIFILOSA, spec. nov. (Figs. 5 and 6).

1 specimen; holotype, M. C. Z. No. 35,067.

Total length 45 mm., standard length 33 mm. Illicium suprafrontal, length from articulation with basal bone to distal end of escal bulb 14 mm. (41% S. L. or 2.4 times as long as the exserted part of the basal bone in the present condition of the specimen[1]). Bulb of esca about 20% of length of illicium from basal bone articulation. Length of lower jaw 14 mm. (41% S. L.); lower jaw with symphysial spine. Large sharp sphenotic spines present; also 2 articular spines on each side, less than half the size of the sphenotics.

Fin rays. D.5, A.5, P.17. Branchiostegal rays 6 (2+4); pectoral radials (pterygials) 3 (1+2).

Dentition. Teeth slender and acicular, depressable inwards. Lower jaw: 24 teeth on each side arranged in three series of different sizes. Upper jaw: 24 in a single series on each premaxillary (only 7-8 of these evident without partial dissection); maxillary toothless. Up-

---

[1] See footnote 2, p. 85.

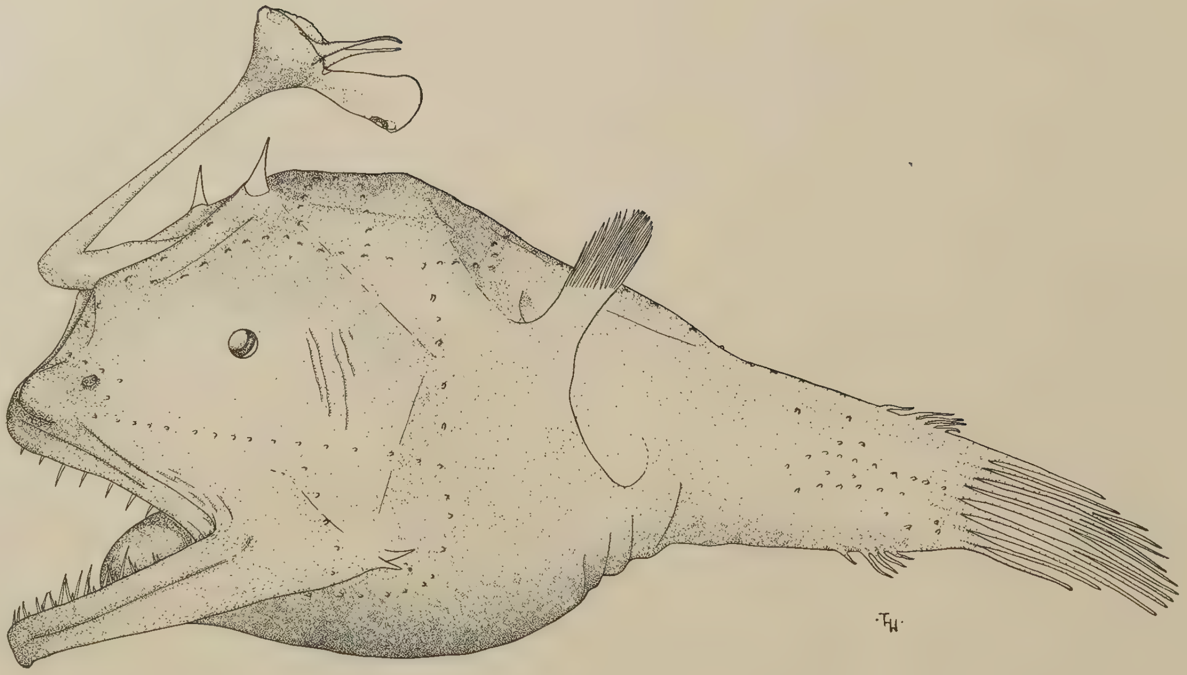


Fig. 5. *Dolopichthys albifilosa*, spec. nov. Standard length 33 mm.

per and lower pharyngeals and palatines toothless. Two teeth on each side of vomer.

The esca[1] (Fig. 6) consists of a laterally compressed terminal expansion of the illicium enclosing within it an ovoid bulb. On the median anterior aspect of the latter is a low papilla projecting anterodorsally. Just posterior to this and running laterally are two slightly raised areas; between these and in the median line is a ridge which runs posteriorly and bifurcates over the posterior portion of the bulb. Each limb of this bifurcation gives rise to a stout, rapidly tapering filament one-fourth as long as the illicium from basal bone articulation to distal end of bulb. A loose transparent layer of tissue covers the distal part of the bulb and terminates posteriorly in a little upstanding ruffle on the antero-median surface of each of the escal filaments. Posterior to the latter and in the median sagittal plane the escal bulb bears a large vane-like, laterally compressed appendage three-tenths as long as the illicium. Distally on the ventral margin of this appendage there is a subspherical heavily pigmented body with a ventrally directed white spot (light organ?). The remaining pigmentation of the whole structure is as follows: the inner bulb of the esca, the proximal part of the latter where it expands from the illicial stem, and the median ridge running posteriorly from the papilla, are all heavily pigmented. The two raised areas just behind and lateral to the papilla, the ventral part of the compressed appendage and the anteromedian aspect of the escal filaments are lightly pigmented by a few scattered granules. The remaining parts of the esca including the rest of the two filaments are whitish.

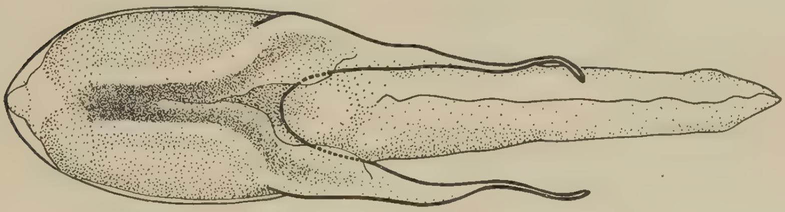


Fig. 6. Dorsal view of esca of *Dolopichthys albifilosa,* spec. nov.

The nostrils are short and tubular with two openings distally; lateral line organs on tags or flaps of pigmented skin with terminal white spots are present on the head and body. An unusual aggregation of these organs occurs caudally between the opposed soft dorsal and anal fins.

---

[1] The present description of the esca is made with the orientation of this organ in the living animal in mind. "Posterior" and "anterior" are reversed in relation to Regan and Trewavas' (1932) use of these terms.

A pelvic bone was found in a dissection of one side of the specimen.

The skin is smooth and jet black.

Type locality. "Atlantis" Station 2667 (35°40′N., 69°36′W.), depth of haul unknown, September 1936.

Discussion

It is clear that the present specimen is closely related to *Dolopichthys nigrifilis* Regan and Trewavas (1932, p. 67). There are, however, a number of distinct differences between them:

1. The escal filaments of *D. albifilosa* are almost entirely free of pigment, whereas the proximal four-fifths of the same appendages in *nigrifilis* are heavily pigmented.[1]

2. These same filaments in the new species are only one-fourth of the length of the illicium from basal bone-articulation to distal end of the bulb; in *nigrifilis* they are about one-half this length or relatively twice as long.

3. In *albifilosa* the stalk of the illicium is heavily pigmented and this pigment runs out distally so far that it covers one-half of the terminal expansion containing the illicial bulb. In *nigrifilis* neither the illicial stalk nor its terminal expansion are so pigmented (Regan and Trewavas, 1932, Fig. 92).

4. The compressed escal appendage in *albifilosa* is somewhat longer relative to the length of the illicium and it is rather more lightly pigmented than it is in *nigrifilis*.

5. The illicium is only 40% rather than 50% of the standard length in the new species.

6. In the present specimen the illicium distal to the basal bone-articulation is only 2.5 times the length of the exserted part of the pterygiophore whereas in *nigrifilis* it is six times this length (see, however, footnote 2, p. 85).

7. The cleft of the mouth in *albifilosa* does not extend posteriorly to the level of the eye whereas it extends behind the eye in Regan and Trewavas' (1932) specimen of *nigrifilis*.

---

[1] It is worth pointing out that the type specimen of *D. albifilosa* was so little damaged when it arrived on deck that it lived for a short time in chilled sea water (see preceding section, p. 71); presumably then such an absence of pigment as mentioned above may well be considered natural rather than due to damage in capturing the specimen.

8. The dentition of the two species would appear to be significantly different; *albifilosa* has 60% more teeth in the upper jaws, and 30% more in the lower than *nigrifilis*. This fact is difficult to evaluate since we do not as yet have any data on the individual or ontogenetic differences in the teeth of ceratioids.[1]

9. The only known specimen of *nigrifilis* is from the China Sea (19°18.5′N.,120°13′E.) whereas *albifilosa* is from the western Atlantic.

The above differences which distinguish the new species from its nearest relative are thus seen to be rather small, and when considered separately some of them are of questionable importance. Nevertheless, they are of the same order of magnitude as those which have been used to establish a great many of the species of this genus (compare, for example, *D. ptilotus*, *D. multifilis*, and *D. claviger* Regan and Trewavas, 1932, p. 73). From the ninety-three specimens of Dolopichthys which have been taken forty-six species have been described; twenty-nine (63%) of them are monotypic. The distinctions between the various members of the genus are, however, of two principal orders of magnitude so that Regan and Trewavas (1932) have distinguished between these by grouping certain of the species differing inter se by such characters as minor variations in the escal pattern into five subgenera which are characterized by differences of a more fundamental nature.[2] In spite of the small amount of material available for comparative study and in spite of the slight variations which have been used in establishing many species, from their wide experience Regan and Trewavas (1932, p. 71) feel that most of the species will prove in the future to be valid.

In view of these facts the establishment of a new species for the present specimen would seem to be quite in keeping with the precedent for the genus.

---

[1] See Fraser-Brunner, 1935, for discussion of evidence for possible ontogenetic changes in the dentition of Gigantactis.

[2] Parr (1934, p. 41ff.) in his revision of the genus Linophryne has accomplished the same sort of distinction between the relative importance of characters by the alternative method of setting up sub-species.

BIBLIOGRAPHY

Boulenger, G. A.

1904. A synopsis of the suborders and families of Teleostean Fishes. Ann. Mag. Nat. Hist., Ser. 7, Vol. 13, pp. 161–90.

Brauer, A.

1902. Diagnosen von neuen Tiefseefischen, welche von der Valdivia-Expedition gesammelt sind. Zoöl. Anz., Bd. 25, S. 277–98.

Brauer, A.

1906. Die Tiefseefische. I. Systematischer Teil. Wiss. Erg. Deut. Tiefsee-Exp. . . . "Valdivia," Bd. 15, Lief. 1, S. 1–420.

Fraser-Brunner, A.

1935. New or rare fishes from the Irish Atlantic slope. Proc. Roy. Irish Acad., Vol. 42B, pp. 319–26.

Gregory, W. K. and G. M. Conrad

1936. The evolution of the pediculate fishes. Amer. Nat., Vol. 70, pp. 193–208.

Parr, A. E.

1934. Report on experimental use of a triangular trawl for bathypelagic collecting. Bull. Bing. Oceanogr. Coll., Vol. 4, Art. 6, pp. 1–59.

Regan, C. T.

1925. New Ceratioid fishes from the N. Atlantic, the Caribbean Sea, and the Gulf of Panama, collected by the "Dana." Ann. Mag. Nat. Hist., Ser. 9, Vol. 15, pp. 561–7.

1926. The Pediculate Fishes of the Suborder *Ceratioidea*. Danish "Dana" Exp., 1920–22, Report No. 2, pp. 1–45.

Regan, C. T. and E. Trewavas

1932. Deep-sea angler-fishes (*Ceratioidea*). Carlsberg Found. Oceanogr. Exp., 1928–30, Report No. 2, pp. 1–113.

Contribution No. 212

Reprinted from THE QUARTERLY REVIEW OF BIOLOGY
Vol. 14, No. 1, MARCH, 1939, pp. 60-64

THE RELATION BETWEEN DIATOMS AND COPEPODS AS A FACTOR IN THE PRODUCTIVITY OF THE SEA

By GEORGE L. CLARKE

Harvard University and Woods Hole Oceanographic Institution (Contribution No. 212)

THE main features of the food-cycle of the sea have been appreciated in a general way for a considerable period. Recently, however, more precise information has been demanded on the exact interrelation of the various organisms depending upon one another for food. These demands have arisen from the discovery that in the case of various economically important animals a failure in a more or less remote link of certain food chains may be responsible for poor production. Accordingly, the whole sequence of events from the penetration of light energy into the water to the growth and distribution of a succession of food organisms must be scrutinized and properly related before the variations in the productivity of the sea can be understood.

One of the essential links in the main food chain of the sea is the copepod group (cf. Clarke, 1934). The traditional impression of copepod production is that it follows and is dependent upon the growth of diatoms. But in attempting to determine more precisely the relations between copepods and diatoms, recent investigators have proposed certain widely differing theories, all of which need confirmation. A comparison of these theories and of the plankton investigations from which they emanate, will be valuable and, it is hoped, helpful in penetrating further into this important problem.

The season sequence of biological events in the Clyde Sea area has been clearly demonstrated by the work of Marshall, Nicholls, and Orr (1934). These investigators studied the time of appearance and the duration of the diatom flowerings and observed the production of successive generations of copepods. In the case of the copepod, *Calanus finmarchicus*, spawning took place at four periods during the year, namely in March, April, May, and July. Three of these spawning periods coincided roughly with times of diatom maxima in this region. The young of the broods originating in these periods grew successfully to maturity, but the brood which was spawned in April, at a time of diatom scarcity, failed to develop. From this, Marshall, Nicholls, and Orr conclude that the presence or absence of diatoms at the critical period of the early life of the copepod means the success or failure of the brood.

In similar investigations off the coast of Norway, Jacob Sømme (*in litt.*) has not found substantiation for this view. On one occasion he observed that the zooplankton, which usually accompanied or followed the spring flowering of diatoms in this locality, preceded the appearance of the diatoms by three weeks, and yet production was successful. Similarly, observations undertaken off Woods Hole by Clarke and Zinn (1937), although of a preliminary nature, did not indicate any necessary dependence of copepod production upon diatom abundance. In our case we found that the two successful spawning periods of *Calanus* occurred at times when the diatoms of the region were at a rather low ebb.

Wimpenny (1936), as a result of a series of observations in the North Sea, regards the presence of the biological conditions which occur within a thick patch of diatoms as particularly important for the successful reproduction of zooplankton. Within his area of investigation he found that the greatest numbers of copepods, particularly *Calanus finmarchicus*, were located between the diatom patches—or at least in no relation to them—whereas the eggs of this species were largely concentrated within these patches. Wimpenny points out that the metabolism of the thickly massed plant cells might be expected to produce an environment attractive to animals ready to spawn and favorable for the development of the newly hatched young. (The actuality of this suggestion has not yet been clearly demonstrated, however). In addition, the abundance of nutriment represented by the diatoms themselves might be a necessary circumstance to bring about spawning, and, if a suitable food, would be important for the nourishment of the feebly swimming young. In short, Wimpenny regards patches of diatoms as nurseries for young copepods and feels that the appearance of the diatoms from May to July is responsible for the successful survival of the new broods. The majority of older copepods, however, were to be found outside the diatom zones.

Certain earlier investigators (Johnstone, 1911; Fish, 1925; and Bigelow, 1926) had reported that in their areas, just as in Wimpenny's case, the main copepod population appeared at times and in places in which prominent diatom flowerings were absent. Renewed interest in this apparent reciprocity of abundance has recently been aroused by the ingenious theories of Harvey and of Hardy. In studying the seasonal succession of events in the English Channel off Plymouth, Harvey and his co-workers (Harvey, Cooper, Lebour, and Russell, 1935) observed that for more than seven months of the year the phytoplankton was consistently scarce during periods when zooplankton was abundant, and vice versa. Harvey presents evidence that the "grazing" of herbivorous plankton animals—chiefly copepods—was sufficient to reduce effectively the number of diatoms present. Some species appeared to eat greatly in excess of their needs when diatoms were abundant. The spring outburst of diatoms was believed limited in quantity and in time by the grazing activity of the zooplankton. According to this theory, then, the copepods are thought of as regulating the plant population.

The theory of Hardy (Hardy and Gunther, 1935), although not irreconcilable with the foregoing, gives quite a different complexion to the relation between copepods and diatoms. Drawing on a large mass of data from his survey of antarctic waters, this investigator suggests that zooplankton definitely avoids areas where phytoplankton is thick. This situation would be brought about if, as Hardy assumes, the upward migration of the zooplankton at night were stopped when a dense diatom population was encountered. For, the animals which occurred under diatom patches, being forced to make a longer daily sojourn in the deeper strata, would be carried away by subsurface currents. As a result of this so-called "animal exclusion," the animals and plants of the plankton would become distributed in alternating communities.

As Hardy has pointed out, both this theory and Harvey's hypothesis may be in operation simultaneously. The zooplankton may be excluded from the centers of the diatom patches because of negative tropistic reactions, but at the same time the animals may reduce the phytoplankton population through grazing around the edges and bottom of the patches. Even if the diatoms are more or less evenly distributed in a given area at the beginning of the productive season, isolated patches would soon be formed by the feeding of local concentrations of zooplankton. The dominant animal type of the region would impress its pattern upon the phytoplankton by "eating holes in it." The distribution of the other species of animals present would then be brought to conform by the action of the "exclusion" process.

In a criticism of these theories, Steeman Nielson (1937) has called attention to a number of cases in which large quantities of both zoo- and phytoplankton exist simultaneously throughout a considerable period. Even in those instances where poor zooplankton has been found in rich diatom zones, or vice versa, a simpler explanation is offered by this author, and one which is particularly apropos for our consideration of causes and limitations of production. It is the time element which Steeman Nielsen shows has been overlooked. He points out that when conditions become favorable for phytoplankton production a very rich population may be established in less than ten days. In the case of the zooplankton, however, not only must the animals mature and spawn following the appearance of suitable conditions, but also a much greater interval must be allowed for development—at least a month for the common copepods. By this time the diatom flowering will probably have passed. Thus arises the impression of an inverse relationship between the animal and plant plankton.

A further complication results from the fact that currents are usually acting on these populations while they are developing. By the time the copepods are fully developed, they may be miles away from the area in which they were spawned. The particularly interesting situation produced by a combination of upwelling and coastal currents off Iceland which is described by Steeman Nielsen, illustrates the necessity for taking the history of the two types of plankton into consideration as well as their distribution at any one time. In general, this investigator concludes that the quantity of zooplankton is directly related to the quantity of phytoplankton, but he emphasizes the fact that because of the slower development of the animals and the effect of currents, a rich growth of diatoms does not necessarity signify the presence in the same locality of an abundant copepod population. The effect of a large phytoplankton production on the zooplankton may appear somewhere else.

This influence of the time element pointed out by Steeman Nielsen is of vital importance, but, in my opinion, its application to the situation has not been carried far enough. An adequate supply of nutriment must be available not only for the maturing parents and for the newly hatched young, but also for each stage of the developing larvae for a considerable time after the spawning period wherever they may drift. In other words, food must be present not alone for the *origination* of the new generation but for its *growth* as well. Careful investigation of the nutritive requirements of copepods has only just begun, but it is reasonable to assume that a considerable supply of food is required at least during the stages in which the animals are increasing in size. Therefore in attempting to explain the distribution of the zooplankton or the success or failure of certain broods on the basis of nutrition, allowance must be made for the food requirements both during the spawning period and subsequently.

Whether or not food organisms were sufficiently available in any given case could be much more conclusively decided if we knew precisely what food marine copepods eat and how much they need. A review of this subject by Clarke and Gellis (1935) showed that early investigators were divided into those believing that the larger diatoms are the chief source of food and those who feel that other elements of the phytoplankton are more important. Our early experiments at Woods Hole on the nutritive requirements of copepods—particularly of *Calanus*—suggested that microörganisms might play a significant rôle (*loc. cit.*). Further investigation of this point showed that bacteria could be ruled out as a possible food source, but left the question open in regard to other types of nannoplankton (Fuller and Clarke, 1936). Since the growth period of *Calanus* off Woods Hole did not coincide with prominent diatom flowerings, Clarke and Zinn (1937) were forced to conclude either (1) that the small number of diatoms always present as a minimum is sufficient, or (2) that the copepods can build up a reserve during local flowerings sufficient to tide them over the intervening periods or (3) that the numerous nannoplankton organisms are important as a food source.

These possibilities introduce the question of the rate at which food is required by copepods. The nutritional demand of a copepod will undoubtedly differ according to its species, sex, age, etc. Furthermore, if, as seems likely from the reports of observers, copepods are omnivorous, the size and composition of the different types of food organisms must be taken into consideration. Doubt has recently been cast by Lowndes (1935) on the view held heretofore that the feeding of copepods is mainly automatic. But even should feeding prove highly selective, a determination of the amount of food required is essential.

Experiments were carried out at Woods Hole by Fuller (1937) to test the factors influencing the rate at which *Calanus* can remove cells of the diatom *Nitzschia closterium* from the water. He found that of the three temperatures tested, namely 3°, 8° and 13°C, feeding was most rapid at 8°. There was some evidence of a diurnal feeding rhythm with greater activity at night. The fact that change in diatom concentration had no effect on the rate of filtration, and other of Fuller's observations, favored the view that feeding in *Calanus* consists of automatic filtering. Since only about one-half of the organic nitrogen content of *Nitzschia* was found to be digested by *Calanus*, the maximum rate of filtering observed was not sufficiently high to permit a copepod to obtain enough diatoms during the day to satisfy its nutritive requirements as calculated by Marshall, Nicholls, and Orr (1935) on the basis of oxygen consumption. However, studies on the growth of individuals which were supplied with different concentrations of diatoms suggested that less food is needed than these measurements indicated. In addition, Harvey (1937) has just published reports of further tests on the feeding rate of *Calanus* in which much larger species of diatoms (*Lauderia* and *Ditylium*) were used. According to these experiments the copepods can "filter out" the larger cells at rates 5 to 100 times greater than was the case with *Nitzschia*.

In most of these laboratory tests the concentration of diatoms used was considerably higher than that ordinarily found in nature. Although calculations indicate that during naturally occurring maxima of the *larger* diatoms food could be obtained rapidly enough to permit growth, long intervals usually exist between such flowerings. The smaller and more numerous types of phytoplankton may then be significant. Furthermore, we do not know whether nauplii of copepods are able to take in the more bulky species of diatoms which generally make up flowerings, since the sizes of food particles suitable for the smaller stages of copepods have not yet been adequately investigated. At certain older stages copepods are able to exist for several weeks without eating—according to our experience at Woods Hole, but we certainly should not expect spawning to take place or the rapid growth of the young nauplii to be possible without a rich supply of suitable food.

Questions such as those left unanswered by the foregoing investigations must be settled before we can hope to follow the course of events involved in the food-cycle of the sea, and to appreciate the delicate adjustments underlying production in an oceanic environment. Further work on this problem had best be undertaken either in a relatively isolated body of water or in such a large, homogeneous area that currents are not a serious disturbance. Proper allowance can then be made for the time element in production. Work could advantageously be pursued in semi-enclosed bays or estuaries, and information derived from inland waters would probably be applicable in part, although in all these cases the effect of the bottom must be taken into consideration. Further laboratory experiments on nutrition should be coördinated with these observations at sea in an effort to determine the exact relation of the variable diatom population to the success or failure of the copepod crop.

Presented at the *Symposium on Hydrobiology* held jointly by the American Society of Zoologists and the Limnological Society of America at Indianapolis, Indiana, on Dec. 30, 1937.

LIST OF LITERATURE

Bigelow, H. B. 1926. Plankton of the off-shore waters of the Gulf of Maine. *Bull. U. S. Bur. Fish.*, 40: 1924, Pt. 2, p. 1–509.

Clarke, G. L. 1934. The Rôle of Copepods in the Economy of the Sea. Fifth Pacific Science Congr., *Vancouver, B. C.*, A5. p. 2017–2021.

Clarke, G. L., and S. S. Gellis. 1935. *The Nutrition of copepods in relation to the food-cycle of the sea. Biol. Bull.*, 68: 231–246.

Clarke, G. L., and D. J. Zinn. 1937. Seasonal production of zooplankton off Woods Hole with special reference to *Calanus finmarchicus. Biol. Bull.*, 73: 464.

Fish, Charles J. 1925. Seasonal distribution of the plankton of the Woods Hole region. *Bull. Bur. Fish.*, 41: Doc. 975.

Fuller, J. L., and G. L. Clarke. 1936. Further experiments on the feeding of *Calanus finmarchicus. Biol. Bull.*, 70: 308–320.

Fuller, J. L. 1937. Feeding rate of *Calanus finmarchicus* in relation to environmental conditions. *Biol. Bull.*, 72: 233–246.

Hardy, A. C., and E. R. Gunther. 1935. The plankton of the South Georgia whaling grounds and adjacent waters, 1926–1927. Discovery Reports, 11: 1–456.

Harvey, H. W., L. H. N. Cooper, M. V. Lebour, and F. S. Russell. 1935. Plankton production and its control. *J. Mar. Biol. Ass.*, 20: 407–442.

Harvey, H. W. Note on selective feeding by *Calanus*. J. Mar. Biol. Ass. 22: 97–100.

Johnstone, J. 1911. Life in the Sea. Cambridge Univ. Press.

Lowndes, A. G. 1935. The swimming and feeding of certain calanoid copepods. *Proc. Zool. Soc. London*, Pt. 3, p. 687–715.

Marshall, S. M., A. G. Nicholls, and A. P. Orr. 1935. On the biology of *Calanus finmarchicus*. VI. Oxygen consumption in relation to environmental conditions. *J. Mar. Biol. Ass.*, 20: 1–28.

Steeman Nielsen, E. 1937. On the relation between the quantities of phytoplankton and zooplankton in the sea. *Jour. du Conseil Perm. Intern. pour l'Exp. de la Mer.*, 12: 147–154.

Wimpenny, R. S. 1936. The distribution, breeding and feeding of some important plankton organisms of the south-west North Sea in 1934. Pt. I. *Calanus finmarchicus*, *Sagitta setosa* and *Sagitta elegans*. *Fisheries Investig. Great Britain.* Ser. II, 15: No. 3, 1936.

Contribution No. 213

The Pituitary Control of Chromatophores in the Dogfish

DR. A. A. ABRAMOWITZ

Reprinted from The American Naturalist, Vol. LXXIII,
pages 208–218, May–June, 1939.

THE PITUITARY CONTROL OF CHROMATOPHORES IN THE DOGFISH*

DR. A. A. ABRAMOWITZ
WOODS HOLE OCEANOGRAPHIC INSTITUTION AND HARVARD UNIVERSITY

THE color changes of elasmobranch fishes were not discovered until about six years ago. In spite of the numerous contributions during this short interval, there exists much diversity of opinion concerning the mechanisms controlling elasmobranch metachrosis. This paper will summarize the various present opinions of chromatic control, and in addition will present some original data which indicate the possibility of a basically uniform plan of chromatic behavior for this group.

The ability to adapt to white or black backgrounds is not shared by all elasmobranchs thus far investigated. These fishes may be roughly divided in this respect into two groups: one showing background responses (macroscopic or microscopic), which are evident within a few hours or a day or longer (*Mustelus canis,* Parker and Porter, 1934; *Raia branchiura, Raia maculata, Rhina squatina, Scyllium canicula* and *Scyllium catulus,* Hogben, 1936; *Squalus acanthias,* Waring, 1938; *Trigon pastinaca, Raia undulata,* Vilter, 1937) and another showing no background adaptation or, at best, limited responses visible only after many days or weeks of exposure (*Raia clavata, Raia batis,* Schaefer, 1921, *Torpedo marmorata,* Veil and May, 1938; *Urolophus testaceus, Trygonorrhena fasciata,* Griffiths, 1936). The first three species of the latter group are more or less persistently dark in tint. No diurnal rhythm of chromatic behavior has been reported in elasmobranchs.

When the pituitary gland or only the neuro-intermediate lobe of this gland is removed, all elasmobranchs thus far investigated become completely pale, due to extreme melanophore contraction, and remain in this condition in environments which elicit darkening in unoperated animals (*Mustelus canis,* Lundstrom and Bard, 1932; *Squalus acanthias,* Lewis and Butcher, 1936; *Scyllium canicula, Raia brachiura, Raia maculata, Rhina squatina, Scyllium catulus, Raia clavata, Raia microcelata,* Hogben, 1936; *Torpedo marmorata,* Veil and May, 1937; *Trigon pastinaca, Raia undulata,* Vilter, 1937; *Raja erinacea,* this paper). However, such hypophysectomized specimens may be darkened temporarily by the implantation of the neuro-intermediate lobe or by the injection of an appropriate extract from this lobe of the hypophysis. From this and other evidence to be pointed out later, all investigators are agreed that the dark phase of elasmobranch color change is due to the production and circulation of the chromatophorotropic hormone (intermedin, "B" hormone, melanophore hormone, etc.) of the neuro-intermediate lobe of the pituitary.

---

* Read at a symposium on "Color Changes in Animals, Their Significance and Activation" at the annual meeting of the American Society of Zoologists in conjunction with the American Association for the Advancement of Science at Richmond, Va., December 29, 1938. Contributions from the Woods Hole Oceanographic Institution, No. 213.

Although investigators are in complete agreement concerning the mechanism controlling the dark phase, no less than four theories have been proposed to account for the induction of the pale or light phase:

(1) That blanching or melanophore contraction is due to the production and circulation of a new hypophyseal hormone—the "W" or melanophore contracting hormone of the anterior lobe of the elasmobranch pituitary (the dualistic hormone theory, Hogben, 1936, Waring, 1938, pertinent to all elasmobranchs).

(2*a*) That paling is due to the direct intervention of melanophore contracting nerves, carrying visual impulses, initiated by a white background, to the melanophores by means of a lipoidal neurohumor as a chemical mediator ("The Nervous Theory," Parker, 1935; pertinent chiefly to *Mustelus canis* and also to *Squalus acanthias*).

(2*b*) That pallor is due to a tonic action of the nervous system allowed expression when the influence of the pituitary is removed or diminished. As in 2*a*, a neurohumor (sympathin) is postulated as a chemical mediator for the induction of melanophore contraction. (Vilter, 1937; pertinent probably to all elasmobranchs).

(3) That pallor is brought about by the diminution or cessation of intermedin secretion during adaptive responses to a white background ("Unihormonal Theory," Lundstrom and Bard, 1932; Parker, 1936–1938; pertinent to *Mustelus canis, Raja erinacea, Squalus acanthias.*

The remainder of this paper will be devoted to an examination of these theories with respect to the original data obtained from experiments on the smooth dogfish, *Mustelus canis.* Such a procedure may be criticized on the general ground that various elasmobranchs differ in their mechanisms of control and, therefore, that a discussion of the group based on results of only one member is unwarranted. However, in *Mustelus,* evidence pertaining to all three main theories has been obtained, and consequently this species has proven to be for the present the most desirable experimental animal.

The responses[1] of *Mustelus* to backgrounds and to certain operative measures are shown in Table I. Although some of these responses have been described fully by Lundstrom and Bard (1932) and Parker (1936–1938), a quantitative tabulation is presented in this paper not merely for the purpose of verification, but chiefly to indicate the extent of variation. Three significant responses may be noted:

(1) That the neuro-intermediate lobe is the only portion of the pituitary, the removal of which results in complete melanophore contraction.

(2) That the removal of only the anterior lobe results in the loss of the white background response.

(3) That the melanophores do not respond directly to light. Concerning the third point, it is true that blinded elasmobranchs are darker when illuminated than when in

---

[1] The diameter of the pigment mass within the melanophores (melanophore diameters) was determined on living fish by means of a calibrated ocular micrometer. 10–25 melanophore diameters were recorded for each fish, and the average taken.

TABLE I

Melanophore Responses in the Pups of Mustelus canis

(After one day adaptation to background)

Condition of animals	White background			Black background			Darkness		
	Number of animals	M.D.	S.D.	Number of animals	M.D.	S.D.	Number of animals	M.D.	S.D.
Normal	5	74	16	10	191	18	4	141	3
Optic nerves cut	4	178	13	4	170	7	4	165	3
Complete hypophysectomy* plus Optic nerves cut	3	32	0.3	2	32	0.5	4	30	2
Complete hypophysectomy	4	29.2	1.0	4	29.2	1.0	5	29.2	1
Neuro-intermediate lobectomy	6	32.4	7.0	5	29.2	3.0	5	27.5	2
Anterior lobectomy	4	186	13	5	196	8	2	181	12
Ventral lobectomy	4	90	8	6	144	24	2	152	32
Sacculus vasculosus extirpated	6	94	36	2	175	13	4	141	37
Neuro-intermediate lobectomy plus sacculus extirpated	2	29.2	0.3	1	37	...	1	32	..

M.D. = Melanophore diameter in micra.
S.D. = Standard deviation in micra.
* = Extirpation of anterior, neuro-intermediate, and ventral lobes, and also sacculus vasculosus.

darkness. The justification of describing this response as a direct effect of light on melanophores (Hogben, 1936; Waring, 1938) is questionable, since it does not occur in blinded, hypophysectomized specimens.

We may now consider the first of the four proposed mechanisms for the induction of the pale phase—the "W" hormone theory.

(1) Extirpation of the Anterior Lobe

The removal of the anterior lobe results in the loss of the white background response, the animals remaining persistently dark in tone in spite of long sojourns on a white background. First demonstrated by Hogben (1936) for *Scyllium canicula, Scyllium catulus* and *Raia brachiura*, this effect has been confirmed by Waring (1938) for *Squalus acanthias,* and in this paper for *Mustelus canis* and *Raja erinacea.* That the loss of the white background response results specifically from the extirpation of the anterior lobe, thereby depriving the animals of a "W" hormone, is doubtful, as reference to Table II indicates. This table shows that the same response may be effected by

TABLE II

EFFECT OF SUPERFICIAL BRAIN LESIONS MADE IN WHITE ADAPTED PUPS (MUSTELUS CANIS) ON MELANOPHORE RESPONSES

(5 animals per group)

Type of lesion	Melanophore diameters in micra				
	On white background			Placed on black on 4th day	Returned to white on 5th day
	Days after lesion				
	1st	3rd	4th	5th	6th
Transverse 1–2 mm between optic chiasma and anterior lobe	243	234	243	243	243
Transverse 1–2 mm anterior to optic chiasma	65	65	49	243	50
Transverse 3–5 mm caudad to pituitary	49	65	65	243	41
2 longitudinal lesions parallel with long axis of anterior lobe (3–5 mm)	40	73	97	243	110
"Denervated" pituitary[1]	240	240	240	240	240
"Implanted" pituitary[2]	240	240	240	...	...
Anterior and neuro-intermediate lobes separated, but not extirpated	162	180	200	180	190

[1] Tongue of anterior lobe dissected free from hypothalamus, then hypophysis completely freed from brain. Hypophysis attached now to brain case by ventral lobe.

[2] Same as above with the exception that anterior and neuro-intermediate lobes also cut free from ventral lobe.

superficial brain lesions made so as to interrupt the probable path of nerve supply (supraoptico-hypophyseal tract) to the intermediate lobe, even when the anterior lobe remains intact. In view of these experimental findings, therefore, the first line of direct evidence favoring the "W" hormone theory loses much of the significance generally attached to results following the surgical removal of an endocrine gland. The results of anterior lobectomy seem explicable as readily on the ground that the mechanism of inhibiting intermediate lobe secretion is interfered with as on the basis that a "W" hormone is no longer available to the melanophores. Certainly, in view of the results listed in Table II, the latter view can not be unequivocally maintained.[2]

(2) REPLACEMENT THERAPY

If the anterior lobe produces a "W" hormone, implants of the anterior lobe or injections of extracts of it should restore the white background response in anterior lobectomized animals. Waring (1938) has found that such measures are wholly ineffective. By other tests (isolated dogfish skin, test on *Xenopus*) Waring (1936) and Hogben (1936) have not been able to demonstrate the presence, in the elasmobranch anterior lobe, of a substance which contracts melanophores.

---

[2] It may be argued that brain lesions affect B and W hormone production differently. My experiments, of course, do not rule out the existence of a W hormone. They do show, however, that for the present the effect of anterior lobectomy must be regarded as non-specific.

(3) Tests for a "W" Hormone in the Blood of Pale Animals

If a "W" hormone is responsible for pallor, its presence in the blood of pale animals should be detectable. Parker (1936–1938) injected blood of pale animals (*Raja erinacea, Squalus acanthias, Mustelus canis*) into dark specimens, without effect on the melanophores of the latter. My own attempts[3] to detect the "W" hormone in the blood of animals possessing intact anterior lobes but lacking neuro-intermediate lobes (such specimens should contain "W" hormone but no "neutralizing" B hormone) have also failed. In these experiments the test blood was injected intramuscularly into animals possessing intact intermediate lobes but lacking anterior lobes.[4]

(4) Differential Tolerance to "B" Hormone

Waring (1938) has shown that *Scyllium canicula,* when injected with a given dose of "B" hormone, will remain dark longer when the anterior lobe is absent than when it is present. This differential tolerance to equal doses of "B" is interpreted as being due to the presence of an antagonistic and neutralizing "W" hormone, hence animals with anterior lobes (and without neuro-intermediate lobes) do not remain dark as long as animals deprived of both lobes. Such a differential tolerance may be explained readily on other grounds: (1) that the anterior lobe may produce a substance inactivating "B" and yet not be a melanophore contracting hormone in itself, and (2), which is more likely, that the change in metabolism following anterior lobectomy in many animals may apply also to elasmobranchs, in which case the differential tolerance would be simply a differential metabolism of the injected "B" hormone.

---

[3] Subcutaneous injections of blood (0.2–0.5 cc) from normal pale, neuro-intermediate lobectomized and completely hypophysectomized animals into dark hosts (normal or anterior lobectomized) always produced pale spots. Sea-water likewise produced pale areas; hence the response is non-specific. None of these effects were produced on intra-muscular injections.

[4] It might be argued that these experiments do not rule out the presence of a "W" hormone in the blood since, by injection of pale blood into dark animals, any "W" present would be neutralized by the antagonistic "B" substance present in the host. Unless insufficient amounts of blood were injected, it is difficult to see how these experiments could otherwise be carried out.

Viewing all the evidence for the dualistic theory, it seems that a "W" hormone has not been demonstrated beyond reasonable doubt. The weakest evidence, peculiarly, results from the direct attack. The circumstantial evidence (differential tolerance curves) is stronger, but explicable on other grounds. The experiments herein reported do not rule out the existence of a "W" hormone. They do indicate, however, that the "W" hormone theory should not, for the present, be accepted until better direct evidence is obtained.

The nervous theory was first formulated by Parker (1935–1938), who discovered (Parker and Porter, 1934) that chisel cuts made transverse to the rays of the pectoral fin or that faradic stimulation of these rays produce pale areas. As a general mechanism of blanching in elasmobranchs, the nervous theory is not applicable, and Parker has limited it to *Mustelus* and possibly to *Squalus,* although not to all individuals of the latter species. Most of the elasmobranchs studied show no nervous control of melanophores. Section of spinal, trigeminal and facial nerves in *Scyllium* sp. has no effect on melanophores (Young, 1933). Similarly, negative effects have been obtained in *Scyllium canicula* by pectoral chisel cuts (Waring, 1936) or by section of spinal nerves (Wykes, 1936); in *Raja erinacea* by pectoral chisel cuts (Parker, 1937); in *Rhina squatina* and *Scyllium catulus* by electrical stimulation of spinal nerves and of the haemal canal (Wykes, 1936); in *Raia maculata* by section of spinal nerves (Wykes, 1936); and in *Raia brachyura* by section of spinal nerves, or by faradic stimulation of spinal nerves or of the haemal canal (Wykes, 1936). In *Squalus acanthias,* electrical stimulation of several rays of the pectoral fin is ineffective in producing pallor (Parker, 1936) but chisel cuts across the rays sometimes produce pale areas (Parker, 1936; Waring, 1938). In *Torpedo,* Vilter (1937) induced pallor by faradic stimulation of the spinal cord. It appears therefore that more evidence has been accumulated for a nerve control in *Mustelus* than in any other elasmobranch, for in addition to cutting and stimulating experiments, Parker (1935) has been able to extract from pale fins a lipoidal neurohumor which he believes to be the chemical mediator to the melanophores.

It must be emphasized that a chisel cut in the pectoral fin of *Mustelus* does more than transect nerves. That the circulation distal to the cut may be interfered with is a criticism that has been repeatedly voiced. Parker has maintained, however, that collateral circulation is evident in the area affected by the cut, but whether this collateral supply is sufficiently normal in its rate of flow and in its total supply is as yet unknown. My studies of the arterial pattern of the pectoral fin indicate that in the area of the fin where cuts are commonly made, it is an anatomical impossibility to avoid severing several radial arteries in denervating by means of a chisel cut. If it could be shown that when nerves are surgically isolated and severed, the area thus denervated would pale, much of the doubt of the interpretation of pale fin bands would be dispelled.

By a dorsal incision over the pectoral girdle of *Mustelus,* the brachial plexus has been exposed and each nerve entering the plexus has been cut, but subsequent pallor in the fin has not been observed. That such an operation denervates the entire fin is seen from resulting immobility of the fin in swimming movements. Even when spinal nerves 1–13 were severed, no paling was observed. On the contrary, background responses may be induced in the denervated fin. Similarly, section of the superficial ophthalmic nerve, on one side or both, produces no paling of the head region. Spinal nerves 21–26 were cut, either consecutively or alternately, but pale areas were not produced. If a chisel cut is made on a denervated pectoral fin, a pale band will appear within 10–30 minutes. If the fin of a dark fish is ligated, the entire fin will pale within 10–30 minutes. But, if a chisel cut is made at the same time the fin is ligated, no pale band will appear. Instead, the entire fin pales uniformly. When the ligature is removed, the fin will darken within 5–10 minutes, but the cut area will remain as a pale band. If a denervated fin is ligated, it will pale within 10–30 minutes.

From these results, it is evident that ligating a fin[5] and making a chisel cut produce the same response in exactly the same time. It is also evident that no melanophore contracting nerves are contained in the brachial plexus at the region of operation. Finally, it appears that if melanophore nerves exist in the pectoral fin of *Mustelus,* they must enter it at some point distal to the region at which the plexus enters the fin. In view of these results[6] showing both the importance of the blood supply and the non-existence of melanophore nerves in the brachial plexus at the point of operation, the nervous control of the pale phase in *Mustelus* can not be accepted wholly until the central connections of such melanophore contracting nerves are found or until histological examination reveals an innervation of the melanophores of this dogfish.

The thesis that melanophores are under a tonic nervous control meets with the same general objection—such nerves must be demonstrated first. An observation by

---

[5] It is possible that ligation of a fin stimulates the nerves by pressure, and hence the melanophores contract. The observation that section of the plexus close to the point where the ligature was made did not produce pallor can not be cited against such a possibility, inasmuch as the melanophore nerves could enter the fin without being contained in the spinal nerves, or if contained in the plexus, at some point distal to entrance of the plexus.

[6] The nerve-cutting experiments involving the brachial plexus were performed on pups, immature and mature specimens. Ligation experiments performed on pups.

Wykes (1936) that pallor is produced uniformly in innervated as in denervated areas following hypophysectomy tends to discredit the tonicity theory. However, the argument that no melanophore nerves are present in the spinal nerves which were cut by Wykes is justifiable, as in the experiments cited above on severing the brachial plexus. But it must be reaffirmed that all attempts to demonstrate the presence of melanophore contracting nerves by surgical measures have failed, and that until this is successfully accomplished, the nervous theory can not be wholly accepted.

The unihormonal theory remains for discussion. Parker (1936–1938) found that defibrinated blood of dark but not pale animals produced melanophore expansion when injected into pale specimens of *Raja erinacea, Mustelus canis* and *Squalus acanthias.* Waring (1938) has also found that more "B" is present in the blood of *Squalus acanthias* during black adaptation than during white adaptation. My own results, although they are still in a preliminary state, are in accord.

Thus the unihormonal theory is the only one in which all the pertinent evidence is in favor of it, and against which there are at present no serious objections. Furthermore, it is the only plan of control which not only applies to those species for which it has been advocated, but which may also function as a basically uniform plan throughout the group. If concentrating nerves are present in *Mustelus,* it is conceivable that pallor is due to the combined action of both nerves and a diminution of intermediate lobe secretion, either of which could produce this effect alone. In any event, it is difficult to evaluate at present the relative significance of nerve control since, on the one hand, normal paling can be accounted for in terms of the pituitary alone, and, on the other, paling can not occur when the pituitary gland is incapacitated by denervation of other measures.

SUMMARY

Of the various theories of control for the color changes in elasmobranchs, the unihormonal theory is at present the

most satisfactory. This mechanism of control was intimated by Lundstrom and Bard (1932) the pioneer investigators in this field, and first clearly expressed and supported by Parker (1936–1938).

REFERENCES

Griffiths, M.
    1936. *Proc. Linn. Soc. N. S. Wales,* 61: 318.
Hogben, L.
    1936. *Proc. Roy. Soc. London,* 120: 142.
Lewis, M. R. and E. O. Butcher
    1936. *Bull. Mt. Desert Island,* p. 20.
Lundstrom, H. M. and P. Bard
    1932. *Biol. Bull.,* 62: 1.
Parker, G. H.
    1933. *Proc. Nat. Acad. Sci.,* 19: 1038.
    1935a. *Biol. Bull.,* 68: 1.
    1935b. *Jour. Gen. Physiol.,* 18: 837.
    1936a. *Proc. Nat. Acad. Sci.,* 22: 55.
    1936b. *Biol. Bull.,* 70: 1.
    1936c. *Biol. Bull.,* 71: 255.
    1937a. *Proc. Nat. Acad. Sci.,* 23: 596.
    1937b. *Proc. Amer. Phil. Soc.,* 77: 223.
    1938a. *Proc. Amer. Acad. Arts and Sci.,* 72: 269.
    1938b. *Proc. Amer. Phil. Soc.,* 78: 513.
Parker, G. H. and H. Porter
    1934. *Biol. Bull.,* 66: 30.
Schaefer, J. G.
    1921. *Arch. ges. Physiol.,* 188: 25.
Veil, C. and R. M. May
    1937. *C. R. Soc. Biol.,* 124: 917.
Vilter, V.
    1937. *Bull. Stat. Biol. Arachon,* 34: 65.
Waring, H.
    1936. *Trans. Liverpool Biol. Soc.,* 49: 17.
    1938. *Proc. Roy. Soc. London,* 125: 264.
Wykes, U.
    1936. *Jour. Exp. Biol.,* 13: 460.
Young, J. Z.
    1933. *Quart. Jour. Micr. Sci.,* 75: 571.

Contribution No. 214

Reprinted from BIOLOGICAL BULLETIN, Vol. LXXVI, No. 3, 371–383, June, 1939
Printed in U. S. A.

THE INFLUENCE OF TEMPERATURE ON THE SURVIVAL, GROWTH AND RESPIRATION OF CALANUS FINMARCHICUS

GEORGE L. CLARKE AND DAVID D. BONNET

(*From the Biological Laboratories, Harvard University, and the Woods Hole Oceanographic Institution*[1])

Experiments which have been in progress at the Woods Hole Oceanographic Institution on the nutrition of the ecologically important copepod, *Calanus finmarchicus,* in relation to the food cycle of the sea have shed light on the types of food suitable for this species and on the rate of feeding of which it is capable under different conditions (Clarke and Gellis, 1935; Fuller and Clarke, 1936; and Fuller, 1937). Since the temperatures to which *Calanus* is subjected off our coasts vary greatly with the season and with the locality, it was desired to extend the investigation of the survival and growth of this species in the laboratory to include a larger range of temperature than had been possible previously. In the earlier experiments survival of the copepods had generally been poor, and Gross (1937) has expressed the opinion that even short intervals of temperature change, such as are entailed by the removal of the culture dishes from the constant temperature bath for inspection, are seriously detrimental to animals in culture. In the experiments about to be described we therefore proposed not only to test the effect of a variety of temperatures on growth but also to compare the survival of animals kept continuously at constant temperatures with that of other individuals subjected to periodic changes in temperature.

Calanus was shown to exist in the waters off Woods Hole throughout the year 1935–36 and to undergo reproduction during the spring months (Clarke and Zinn, 1937). Yet food organisms were not sufficiently abundant in these waters to meet the nutritive requirements which we have assumed for *Calanus* even at the maximum rate of feeding observed in the laboratory, if diatoms alone are considered (Fuller and Clarke, 1936; and Fuller, 1937). Food in the form of diatoms appeared to exist in only one-tenth the necessary concentration. This discrepancy has led to such suggestions as the considerable use of the nannoplankton by the copepods and this possibility should be investigated further, but the difficulty could be removed equally well if the value assumed for the food requirements of *Calanus* were shown to be ten times too high. The value used was that given by Marshall, Nicholls and Orr (1935) and was calculated from the amount of oxygen taken up by a given number of copepods in unit time. The confirmation of this work was therefore of the greatest importance and we proposed in the present undertaking to repeat the measurements of these investigators, using their own method, and to check them by employing a more precise method. Furthermore, we desired to ascertain whether differences in temperature exert any significant effect on the oxygen requirement of *Calanus* and its application to the nutrition of this species.

---

[1] Contribution No. 214.

SURVIVAL AND GROWTH

Material and Methods

For the first group of experiments, which was conducted at Woods Hole during the summer of 1937, copepods were obtained from offshore localities in the vicinity of Cape Cod. In the second group of experiments, which was undertaken at the Harvard Biological Laboratories in Cambridge, material was obtained off Gloucester. In all cases the copepods were collected by towing a scrim net for a few minutes, and were placed in jars which were kept cold during the trip to the laboratory. Immediately upon arrival the animals were transferred by means of a pipette to covered culture dishes and these were set in baths whose temperature was maintained constant to within 0.5° C. In all the experiments except those involving a change of temperatures (see below) the copepods were transferred each day by pipette to freshly prepared culture dishes (each containing 250 cc. of water) which had been brought to the proper temperature.

The sea water used in the Woods Hole experiments was taken freshly from the harbor (except for the experiments of Table II); that used in Cambridge had been collected at Nahant several months previously and allowed to stand in carboys. In both instances the water was Berkefeld filtered (except for a few tests at Woods Hole in which unfiltered harbor water was used) and then thoroughly aerated.

In most of the experiments a known concentration of food was provided by adding a measured amount of a " persistent " culture of either the diatom, *Nitzschia closterium* (Plymouth strain) or the green flagellate, *Platymonas subcordiformis*[2] to each culture dish. The amount of organic matter represented by these forms and also by the diatom, *Rhizosolenia* sp., which was abundant in Woods Hole waters during the summer, may be judged from the following determinations of nitrogen kindly carried out for us by Dr. T. von Brand:

---

[2] Kindly identified for us by Professor G. W. Prescott of Albion College, Michigan.

Nitzschia	2.5	γN	per	10^6	cells[3]
Platymonas	12.7	"	"	"	"
Rhizosolenia	96.0	"	"	"	"

To ascertain whether the number of animals present or the concentration of food organisms was sufficient to affect significantly the dissolved oxygen or the pH of the culture medium, tests were carried out on a representative series of culture dishes as indicated in Table I. The results show that sufficient O_2 was present in all containers and that the pH was only slightly altered. The slight increase in O_2 content and decrease in pH in the control was due to incomplete temperature equilibrium initially.

TABLE I

Tests of pH and O_2 in culture dishes with different numbers of copepods and of food organisms.

Concentration of Nitzschia cells/cc.	Number of Stage V Calanus	pH		O_2 cc./liter	
		Initial	After 24 hrs.	Initial	After 24 hrs.
0	0	8.09	7.86	4.25	5.67
0	10	8.09	7.81	4.25	6.42
30,000	0	8.11	9.09*	4.68	5.94
30,000	10	8.11	7.73	4.68	6.65
300,000	0	8.17	8.10	4.81	6.49
300,000	10	8.17	8.00	4.81	6.37

* This value shown by other tests to be atypical.

Experiments

The first set of experiments was designed to ascertain whether the *change* in temperature which results from the removal of the culture dishes from the constant temperature bath for daily inspection and transfer of animals has a deleterious effect on the copepods. For this purpose groups of *Calanus* and also of *Centropages typicus*—another copepod common in the Woods Hole region—were divided into two parts and placed in culture dishes in constant temperature baths maintained at either 8° C. or 13° C. One culture dish in each group was left undisturbed in the bath as a control but others were removed for varying lengths of time as indicated in Table II. For the duration of the experiments the survival of *Calanus* was better than that of *Centropages* but in neither case was survival in the control dishes significantly better than that in the dishes which were subjected to a daily temperature change. We conclude, therefore, that contrary to the suggestion of Gross (1937), the daily inspection at room temperature is not harmful in our experiments with these copepods.

---

[3] The reason why this value is larger than that found the year before and reported by Fuller (1937) is not known. Variations of this sort must be taken into consideration in calculating the potential food value of each species.

Our next set of experiments was designed to test the effect of the concentration of food organisms on the survival and growth of *Calanus* at temperatures of 7° or 8° C. For this purpose culture media were prepared in which the concentration of food organisms differed by very large amounts (Table III). Ten to twenty-five *Calanus* were introduced into each culture dish and their condition noted each day for the duration of the experiments (2 to 4 weeks). The daily transfer of animals to freshly prepared culture media prevented an appreciable change in the concentration of the food from being brought about by either the grazing of the animals or the multiplication of the food organisms. Accumulation of metabolites was similarly avoided.

TABLE II

Effect of *change* of temperature on survival. Comparison of number of deaths in cultures removed from constant temperature bath for daily periods of varying lengths with number of deaths in cultures not removed. Two hundred and fifty cc. Berkefeld filtered sea water from tap in each culture dish, left unchanged, and no food added. Experiments carried out in July, 1937 at Woods Hole.

Species	Initial no. of animals in each culture dish	Temp. of constant temperature bath	Period culture removed from bath each day	Temp. of culture when replaced	Duration of experiment	No. of deaths
		° C.		° C.	*days*	
Calanus (Adults)*	10	8.5	30 minutes	14.0	8	1
" "	10	8.3	not removed		8	3
Calanus (Stage V)†	15	8.0	60 minutes	16–19	7	0
" "	15	8.0	not removed		7	1
Centropages (Adults)*	20	8.5	30 minutes	12–15	8	17
" "	22	8.5	120 "	16–21	8	15
" "	20	8.2	not removed		8	12
" "	20	13.3	30 minutes	15–18	8	18
" "	20	13.3	120 "	20–21	8	20
" "	20	13.0	not removed		8	18

* Animals obtained at Whistle Buoy at western entrance to Vineyard Sound.
† Animals obtained at South Channel, east of Nantucket.

In this set of experiments no copepods were observed to moult successfully but certain individuals reached the moulting stage and died during the casting of the shell. As in previous investigations, the number of animals which began the moulting process may be taken as an index of growth. The reliability of this procedure is strengthened by the fact that low numbers of " deaths in moult " are usually accompanied by high numbers of " deaths not in moult " and vice versa (see Table III). On this basis our results reveal the best nutritional conditions in those cases where 30,000 cells/cc. of *Nitzschia,* or more, were provided, but a concentration as high as a million and a half cells/cc. appeared harmful. The moulting stage was attained (i.e. " deaths in moult ") in a higher proportion of cases in the tests begun on July 11 than in those begun on August 15 and in the experiment of September 11 not a single copepod reached the moulting condition. Indication that the animals stopped feeding toward the end of the season arises from the fact that no significant difference was observed in the survival in different food concentrations for the September 11 experiment. Moreover, in this case and in the experiment of August 15 the unfed controls fared as well or better than the copepods which were provided with

TABLE III

Effect of concentration of food on survival of *Calanus.* Temperature of constant temperature bath for experiments in July and August: 8° C., in September: 7° C. Each group of animals placed in 250 cc. of culture medium. Animals in copepodid Stage V. Experiments conducted at Woods Hole in 1937.*

Food organism	Conc. of food	Exper. begun	Exper. concluded	Initial no. of copepods	Deaths in moult	Deaths not in moult
	cells/cc.					
Nitzschia	300,000	July 11	Aug. 9	15†	8	5
"	150,000	"	"	15	10	4
"	30,000	"	"	15	8	3
"	15,000	"	"	15	4	8
none		"	"	15	4	8
Nitzschia	1,500,000	Aug. 15	Aug. 31	25‡	0	25
"	150,000	"	Sept. 3	25	1	13
"	1,500	"	"	25	4	16
none		"	"	25	0	11
Unfiltered	harbor water	"	"	25	0	22
Platymonas	18,000	Sept. 11	Sept. 31	10‡	0	7
"	4,500	"	"	10	0	6
Nitzschia	230,000	"	"	10	0	9
none		"	"	10	0	6

* Experiment begun September 11 carried out with the assistance of Mr. Dean F. Bumpus, biological technician for the Woods Hole Oceanographic Institution.

† Animals obtained from South Channel, east of Nantucket.

‡ Animals obtained from Cape Cod Bay, 4 miles NNE of Canal.

food. This suggests that the feeding or the survival (or both) of the copepods may depend upon the season because of differences in the phase of the life cycle characterising the copepods at the time the experiments were begun (see below).

With the possibility of a seasonal effect in mind, arrangements were made for the next set of experiments to be conducted during the spring months when *Calanus* off our shores is known to be breeding and growing (Fish, 1936; Clarke and Zinn, 1937). In nine tests at three temperatures and with varying amounts of food using copepodid stage IV and in three tests using copepodid stage III, run in exactly the same manner as the experiments of the previous summer, survival was good and a considerable amount of moulting took place (Table IV). In the case of stage IV the number of successful moults at 3° C. did not differ materially with the amount of food provided, but at the other

TABLE IV

The effect of temperature and food concentration on the survival and growth of *Calanus*. Animals obtained off Gloucester. Each group placed in 250 cc. of culture medium. Experiments conducted at Harvard Biological Laboratories in 1938 with the assistance of Mr. Dean F. Bumpus.

Jar	Temp.	Conc. of Nitzschia	Initial population April 22. Copepodid stage	Successful moults	Deaths in moult	Deaths not in moult	Final population May 18. Copepodid stage
		cells/cc.					
1	3° C.	150,000	10 IV	5	0	1	1 IV, 7 V†
2		1,500	8 IV, 2 III	4	0	2	2 IV, 6 V
3		0	9 IV, 1 III	5	0	3	2 IV, 4 V†
4	6° C.	150,000	11 IV	10	0	5	3 V, 3 VI♂
5		1,500	10 IV	6	0	5	3 V, 1 VI♂, 1 VI♀
6		0	8 IV, 2 III	0	1	9	0
7	9° C.	150,000	9 IV, 1 III	7	1	4	1 V, 1 VI♂, 2 VI♀†
8		1,500	10 IV	5	1	5	3 V, 1 VI♀
9		0	10 IV	2	1	8	1 V
10*	3° C. then 9° C.	1,500	10 III	4	1	6	2 V†
11	6° C.	1,500	10 III	2	2	7	1 V
12	9° C.	1,500	10 III	6	0	1	?‡

* At the end of 7 days at 3° C. no animals had moulted and none had died. The jar was then transferred to 9° C.

† One animal missing.

‡ Animals accidentally lost on the seventh day.

temperatures a distinct positive relation was found between the growth of the animals and the concentration of *Nitzschia.* The largest number of animals moulting occurred in the culture with high food concentration at 6° C. (Jar 4). Deaths during moult took place chiefly at the high temperatures. Deaths not in moult were much more abundant in the cultures not provided with food and were confined largely to the higher temperatures.

Of the stage III animals, all of which were provided with the same amount of food, the group at 9° C. was accidentally lost on the seventh day but six in this group had already moulted. In contrast, there were no signs of growth by the seventh day in the group at 3° C. However, after the latter animals had been transferred to the 9° bath, four moults occurred within six days. In the culture at 6° C. there were two successful moults and two deaths in moult. Three of the stage III animals attained stage V, thus having passed through two moults. In the case of the copepods which were in stage IV at the beginning of the experiment, nine individuals (in the 6° and 9° cultures) moulted twice and thus reached the adult condition (stage VI).[4] From the results of this set of experiments we may conclude that at 3° C. moulting was retarded but at the same time survival was good. A larger number of successful moults and deaths in moult occurred at 6° C. and about the same proportion at 9° C. but at these temperatures survival was definitely inferior to that at 3° C.

RESPIRATION

Material and Methods

The copepods used for the experiments on respiration were taken by tow net in Cape Cod Bay and placed in large jars packed in ice for the return run to the laboratory. Vigorous specimens of copepodid stage V were then picked out by pipette, transferred to culture dishes and placed in the refrigerator at 8° C. until the tests were begun on the following day. The sea water used for the cultures and for the experiments was taken in carboys at the point where the animals were collected (except for the tests at 16.8° C. in which the laboratory salt water supply was used). In all cases the sea water was Berkefeld filtered and aerated before use. No food was added.

Respiration was measured by the Winkler method and in other tests by a manometric method in which a respirometer of the Dixon-Haldane constant pressure type was used. In the former case almost exactly the same procedure was followed as that described by Marshall, Nicholls, and Orr (1935) except that in the tests reported below 25 and

---

[4] Under the microscope the gonads of both sexes were observed to be ripening at the end of the experiment.

75 animals were used respectively in 200 cc. of water instead of the 120 animals employed by the earlier workers. In the latter case the apparatus was arranged as outlined by Dixon (1934) with the exception that no KOH well for the absorption of CO_2 was used. Tests showed that no difference in the changes of value of the gas within the apparatus occurred when the KOH well was removed. It is probable that over the short periods of time involved the small amount of CO_2 produced was readily absorbed by the slightly alkaline sea water. In our apparatus all joints were of ground glass and were carefully sealed with stopcock grease or vaseline. The respiration flasks were completely immersed in a constant temperature bath controlled to 0.5° C.

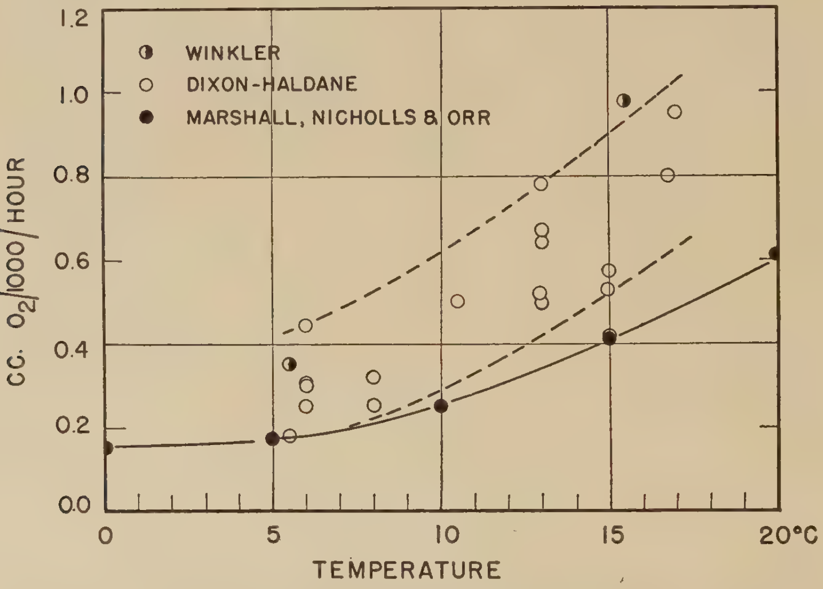


FIG. 1. Relation between temperature and amount of oxygen consumed by stage V *Calanus*. Dashed lines give the limits of all determinations with the Dixon-Haldane respirometer. Experiments carried out at Woods Hole during August and September, 1938.

In the experiments which follow 6 to 30 animals were placed in 10 to 20 cc. of water in one of the respiration flasks. This flask had been painted black to exclude light since Marshall, Nicholls, and Orr reported that differences in illumination exerted a marked influence on the rate of respiration. Equilibrium between the liquid and the gas above it was attained by attaching the entire apparatus to a Warburg shaker. Since continuous or rapid shaking resulted in poor survival of the copepods and might influence abnormally the rate of respiration, the shaking was limited to the 5 or 10 minutes immediately before each reading and was confined to an amplitude of 2 cm. at a frequency of 100/min. Readings were ordinarily made every 20 minutes for 4 or more hours. The change in volume for each period was observed and reduced to cc. dry gas at N. T. P. Blank trials, which were run at intervals in exactly the same way but with no animals, showed no variation in volume over periods as long as 4 hours. In certain cases water in which copepods had been living and which presumably contained a characteristic number of bacteria was used for the blank tests. Thus assurance was provided that in the experiments neither microörganisms nor other extraneous agents were interfering appreciably with the results.

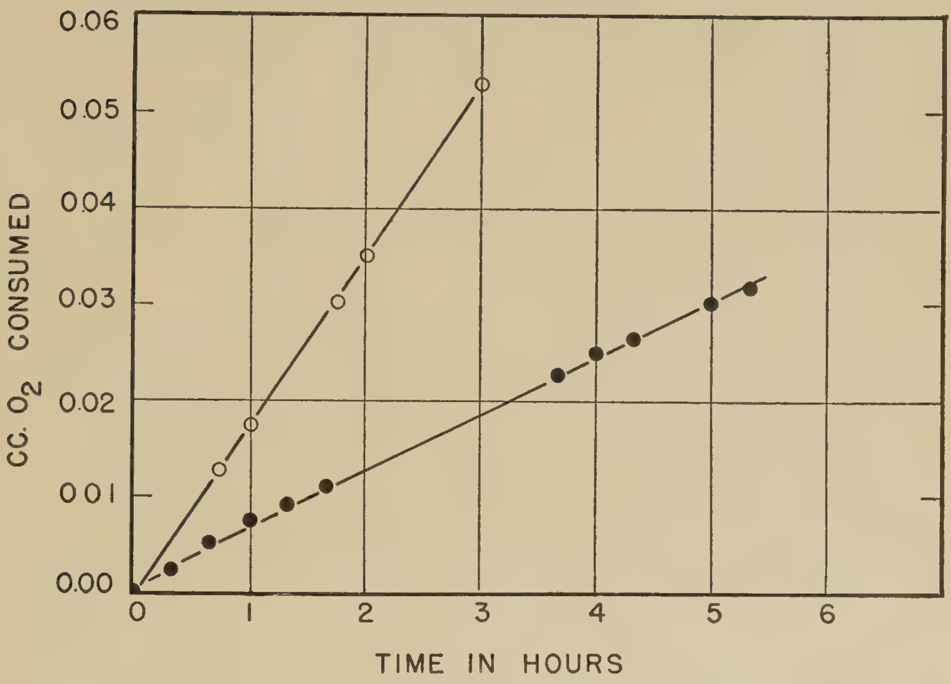


FIG. 2. Progress of two typical experiments on consumption of oxygen by stage V *Calanus*. Closed circles: 6 animals at 16.8° C. Open circles: 28 animals at 13.0° C.

Experiments

Two measurements of the oxygen consumption of *Calanus* were made using the Winkler method. The first of these was carried out at 5.5° C. using 25 animals confined in 200 cc. of sea water for 4 hours and yielded a value of 0.35 cc. O_2/hr./1,000 copepods. In the second case 75 animals in 200 cc. were tested at 15.5° C. for 4 hours and were found to have consumed oxygen at the rate of 0.98 cc. O_2/hr./1,000 copepods. The first of the values is somewhat higher and the second is considerably higher than those obtained by Marshall, Nicholls, and Orr (1935), as may be seen in Fig. 1.

The experiments using the Dixon-Haldane respirometer comprised 17 tests carried out at 7 temperatures ranging from 2.5° C. to 16.8° C. In each test from 4 to 12 readings were made during the course of the run and these were plotted against time, as in the two typical experiments shown in Fig. 2. The fact that these curves and all the others which have been used in the calculations exhibited only a slight deviation from a straight line shows that the consumption of oxygen was sensibly constant over the period of each experiment. Marshall, Nicholls, and Orr reported a drop in oxygen consumption during the first 10 or 15 hours after the capture of the copepods but in our experiments, since measurements were not begun until the day following capture, this period of decreasing respiration was avoided.

From the average slope of each curve of oxygen consumption a value was obtained which was converted into cc. O_2/hr./1,000 copepods and the results plotted in Fig. 1. It will be observed that a considerable variation exists among the several tests at the same temperatures. Evidently respiration in *Calanus* can vary between wide limits and this conclusion is borne out by the observations of the earlier investigators. However, there is no doubt as to the general magnitude of the oxygen requirement of *Calanus* in the present experiments. The influence of temperature on respiration is indicated by the upward slope of the dashed lines in Fig. 1 enclosing all the points. The values increased from an average of about 0.32 cc. O_2/hr./1,000 copepods at 5.5° C. to about 0.91 cc. O_2/hr./1,000 copepods at 16.8° C. Although our measurements give a somewhat higher average rate of respiration at all temperatures than was obtained by Marshall, Nicholls, and Orr, they are of the same order of magnitude. Furthermore, there is no indication of a possible lower oxygen requirement for the Woods Hole copepods since *every one* of the present values was higher than those obtained by the British investigators.

Discussion

The foregoing experiments not only have confirmed and illuminated the early work at Woods Hole, but in addition have raised a number of new questions. It is clear that both the amount of food and the temperature have an important influence on the growth of *Calanus* and on its survival.[5] The situation is further complicated by the fact that under conditions which tend to promote growth, survival may be poor because of the likelihood of death during the moulting process. The provision of food improves growth and survival, but the exact amount of food seems not as important as originally supposed (cf. Clarke, 1939). Although a minimum was ordinarily required for growth, in certain experiments at low temperatures some moulting was observed in the entire absence of food. And in at least one case a very high concentration of food was found to be harmful (see also Lucas, 1936).

It is a striking fact that a large amount of moulting took place and good survival was observed in our experiments conducted in April and May (Table IV) whereas poor survival and no successful moulting was the rule for the tests made during the summer and early autumn (Table III) and for the summer experiments of Fuller (1937, Table V, temperature 13° C.).[6] In all cases *Nitzschia* was used as the food organism in at least some of the cultures, the temperatures of the cultures were not widely different, and exactly the same procedure was followed. For the April and May tests copepods were obtained from a point off Gloucester but in two of the other cases the experimental animals were procured from a location which was also north of Cape Cod although considerably to the south of Gloucester.[7] If the place of origin of the copepods is immaterial, it might be suggested that the time of year at which the animals were collected could have an important bearing on the laboratory results. According to the observations of Clarke and Zinn (1937) and of Fish (1936) the second of the two yearly broods of *Calanus* grows to copepodid stage V during the summer and remains in that stage until the following January or February. It seems possible that in nature feeding may be reduced to a minimum and mortality may be especially high during the late summer and that animals collected during this period might exhibit poor survival and refuse to grow even under the most favorable laboratory conditions. Added support for this view is derived from the fact that in our experiment begun September 11 (Table III) no successful moults occurred and no animals were observed even to attempt to moult.

[5] In fact Fish (1937) is of the opinion that the presence of suitable temperatures is the most important factor in the production of zoöplankton in the Gulf of Maine and the Bay of Fundy.

[6] In the earlier summer experiments of Clarke and Gellis (1935) and of Fuller and Clarke (1936) growth and survival were better, but the different methods used make comparisons inappropriate.

[7] The following ocean temperatures were observed:

Off Gloucester, April 26, 1938, 9.6° C. at surface.
Cape Cod Bay, August 14, 1937, 18.3° C. at surface, 10.2° C. at 15 m., 8.6° C. at 30 m.
South of Cape Cod temperatures were generally higher.

In all of our experiments at Woods Hole and especially in those described above the copepods were noticed to be heavily parasitized immediately after death. An animal which appeared perfectly healthy one day would be found dead on the next day with its body filled with opaque whitish or colored masses. Possibly parasites gain a foothold within the copepod and remain unnoticed until they suddenly reach some vital tissue. From this initial infection the rapid and obvious spread of the parasite to all parts of the body could be accomplished after death within a relatively short interval. Since Jepps (1937) reported that a large proportion of *Calanus* population was found to be infected when collected, it is possible that the inroads of parasites may be an important element underlying the fluctuation in the abundance of this species both seasonally and annually.

The experiments on respiration show that the values which have been used for the oxygen consumption of *Calanus* and hence its food requirement, are of the correct order of magnitude. In fact, our measurements indicate that an even larger amount of food per day is required by these organisms than was assumed by Marshall, Nicholls, and Orr. Therefore, the discrepancy between the nutrient required and the number of diatoms available for food gapes wider than ever. According to Harvey (1937) *Calanus* can filter out the larger species of diatoms much more effectively than the smaller forms. He found that 100 times the volume of water may be swept free in an hour when *Lauderia* or *Ditylium* were provided as food as when *Nitzschia* was used. However, in nature the larger diatoms are not as abundant as the more minute species, and a careful investigation of the amount of food per cc. of sea water which the scarcer but more bulky types would provide is seriously needed. Another point which needs study is the " micro-distribution " of the phytoplankton and nannoplankton. Although uniformity in abundance may be found in a series of one-liter water samples taken from an area, the distribution *within* each liter may be highly irregular. If the food organisms occur in clusters, and if a copepod can find and stay in a local though minute zone of abundance, sufficient nutriment could be obtained without the necessity of filtering an excessive volume of water. Such explanations as the foregoing may resolve the discrepancy between the daily food requirement and the *average* abundance of potential food organisms.

SUMMARY

Laboratory tests on cultures of *Calanus* in relation to the ecology of this species showed that: (a) removal of the culture dishes from constant low temperature to room temperature for daily periods as great as 120 minutes was not harmful to the copepods; (b) growth was poorer at 3° C. than at 6 to 9° C. but survival is better at the lower temperatures; (c) both growth and survival decreased regularly in passing from experiments conducted in the spring to those in the autumn.

Measurements of the respiration of *Calanus* using the Winkler method and the Dixon-Haldane respirometer showed that the magnitude of the oxygen requirement for our animals is of the same order as for those tested by Marshall, Nicholls, and Orr, and possibly is higher than previously reported. The discrepancy between the estimated food requirement of *Calanus* and the average abundance of diatoms therefore still exists but certain possible explanations are discussed.

REFERENCES

Clarke, G. L., 1939. The relation between diatoms and copepods as a factor in the productivity of the sea. *Quart. Rev. Biol.,* in press.

Clarke, G. L., and S. S. Gellis, 1935. The nutrition of copepods in relation to the food-cycle of the sea. *Biol. Bull.,* **68**: 231–246.

Clarke, G. L., and D. J. Zinn, 1937. Seasonal production of zoöplankton off Woods Hole with special reference to Calanus finmarchicus. *Biol. Bull.,* **73**: 464–487.

Dixon, Malcolm, 1934. Manometric Methods. Cambridge University Press.

Fish, C. J., 1936. The biology of Calanus finmarchicus in the Gulf of Maine and Bay of Fundy. *Biol. Bull.,* **70**: 118–141.

Fish, C. J., and M. W. Johnson, 1937. The biology of the zoöplankton population in the Bay of Fundy and Gulf of Maine with special reference to production and distribution. *Jour. Biol. Board of Canada,* **3**: 189–321.

Fuller, J. L., 1937. Feeding rate of Calanus finmarchicus in relation to environmental conditions. *Biol. Bull.,* **72**: 233–246.

Fuller, J. L., and G. L. Clarke, 1936. Further experiments on the feeding of Calanus finmarchicus. *Biol. Bull.,* **70**: 308–320.

Gross, F., 1937. Notes on the culture of some marine plankton organisms. *Jour. Mar. Biol. Ass'n,* **21**: 753–768.

Harvey, H. W., 1937. Note on selective feeding by Calanus. *Jour. Mar. Biol. Ass'n,* **22**: 97–100.

Jepps, M. W., 1937. On the protozoan parasites of Calanus finmarchicus in the Clyde Sea area. *Quart. Jour. Micros. Sci.,* **79**: 589–658.

Lucas, C. E., 1936. On certain inter-relations between phytoplankton and zoöplankton under experimental conditions. *Jour. du Conseil Int. pour l'explor. de la mer,* **11**: 343–362.

Marshall, S. M., A. G. Nicholls, and A. P. Orr, 1935. On the biology of Calanus finmarchicus Part VI. Oxygen consumption in relation to environmental conditions. *Jour. Mar. Biol. Ass'n,* **20**: 1–28.

Contribution No. 216

Reprinted from the AMERICAN JOURNAL OF BOTANY, Vol. 26, No. 6, 399–407, June, 1939
Printed in U. S. A.

THE ABSORPTION OF PHOSPHATE AND NITRATE BY ILLUMINATED CULTURES OF NITZSCHIA CLOSTERIUM[1]

Bostwick H. Ketchum

THE RESEARCHES of Brandt (1899, 1902) first called attention to the importance of phosphate and nitrate as factors limiting phytoplankton growth in the sea. Numerous investigations have since been made using accurate analytical methods, and the results show that during the growth of the phytoplankton, phosphate and nitrate may be removed completely from the water (Atkins, 1923, 1926a, 1926b; Cooper, 1933; Harvey, 1926, 1928; Harvey et al., 1935; Kreps and Verjbinskaya, 1932; Marshall and Orr, 1928). Some results indicate that the growth of phytoplankton ceases when these ions have completely disappeared from the water (Marshall and Orr, 1928).

The conclusions reached by study of the variables in the sea have been corroborated by laboratory experiments. Schreiber (1928) determined the total number of diatoms which could be grown in water collected at various times of the year and found a good correlation between the concentration of phosphate and the crop. Braarud and Foyn (1931) showed that nitrate can also limit diatom growth.

Although the concentrations of phosphate and nitrate in sea water vary between wide limits, Redfield (1934) showed that they vary in a related fashion. The ratio of concentrations in the waters of the West Atlantic, South Atlantic, Pacific, and Indian Oceans and Barents Sea is about one atom of phosphorus to twenty atoms of nitrate nitrogen. Redfield also shows that the proportions of carbon, nitrogen, and phosphorus in typical hawls of various plankton are nearly the same as the proportions found in the sea water. He pointed out that these relations do not obtain in water bodies of limited extent, such as the English Channel, the Gulf of Maine, etc., where local conditions may alter the picture. Cooper (1937) discusses the departure from the usual ratio in the English Channel and in the Mediterranean Sea but offers no explanation for these anomalies.

Redfield (1934) states: "Whatever its explanation, the correspondence between the quantities of biologically available nitrogen and phosphorus in the sea and the proportions in which they are utilized by the plankton is a phenomenon of the greatest interest."

The absorption of phosphate and nitrate by pure cultures of a marine diatom has been studied to determine what effect its growth might have upon the ratio of these ions in the water. This paper presents data relating the absorption of phosphate and nitrate by cells grown under continuous illumination to the concentration of these ions in the medium. In those ranges of concentration normally found in the sea the rate of absorption per cell is dependent on the concentrations of the nutrient in the water. The rate of phosphate absorption is dependent on both the nitrate and the phosphate concentration, while the rate of nitrate absorption is dependent on the concentration of nitrate in the medium and independent of the phosphate concentration.

As a consequence of this relationship the ratio in which phosphate and nitrate are absorbed is dependent on the concentration of phosphate in the medium and independent of the nitrate concentration over large ranges. The growth of the cells changes the proportions in which phosphate and nitrate are present in the medium. Under certain conditions the metabolism of the cells brings the ratio of phosphorus to nitrogen closer to the usual value found in the sea; under other conditions it increases an original departure from this ratio.

MATERIAL AND METHODS.—The marine diatom, *Nitzschia Closterium,* which was used in this work was grown in the medium suggested by Ketchum and Redfield (1938). Stock cultures in 500 cc. Erlenmeyer flasks were prepared regularly and were grown in the light of a north window. These cultures were seeded with a concentration of 50,000 cells per cc. and contained, at the end of five or six days, about two million cells per cc. At this time they were used as seed for the new stock and for the experimental work. Tests for bacteria were made regularly by plating on the medium described by Reuszer (1933), as well as by the methods suggested by Barker (1935a). All the experiments described were performed on bacteria-free cultures.

The phosphate in the medium was measured by the Deniges-Atkins ammonium molybdate method, using stannous chloride as the reducing agent (Atkins, 1923). Since the cells present in the medium give the solution a greenish color which will not match with the standards, the cultures were filtered through a barium sulphate precipitate on a cintered glass filter, as suggested by Redfield, Smith, and Ketchum (1937). Salt effect and blank corrections were always made (cf. Redfield et al.).

---

[1] Received for publication April 4, 1939.
Contribution No. 216 of the Woods Hole Oceanographic Institution.
The author expresses his sincere thanks to Professor Alfred C. Redfield, who suggested this problem, for his generous assistance and advice.

The nitrate nitrogen in the medium was measured by the reduced strychnine method described by Harvey (1926) for use in sea water. The modifications introduced by Rakestraw, as discussed by Wattenburg (1937), were used throughout. The color was allowed to develop for eight hours and was compared in a bicolorimeter with standards consisting of methyl orange in 0.001 normal HCl. Concentrations ranging from 5 to 100 gamma (grams $\times 10^{-6}$) of nitrogen per liter can be measured directly. Higher concentrations must be measured by dilution with "nitrate free" sea water. Corrections were made for the amount of nitrate added in the diluting water. The reagent measures both nitrate and nitrite nitrogen. The latter is always present in relatively low concentrations, and nitrate was used for enrichment of the culture medium. The measurements were recorded, therefore, as nitrate. All figures given in the paper are the average of two or more check analyses.

The experimental cultures were grown in a specially constructed air chamber. An electric refrigerating unit is set into one-half of the top of an insulated box. The other half is occupied by a window consisting of two sheets of glass, separated by one and one-half inches of insulating air space. The inner sheet is finely ground in order to diffuse the light. The light source consists of four 100-watt lamps mounted on the corners of a twenty-inch square of plywood, the center of which is occupied by a 75-watt bulb. The bulbs are an inch above the outer glass plate. The cultures are supported by a shelf within the chamber ten inches below the glass window. This lighting arrangement gives uniform illumination on the shelf which is more than adequate to produce maximal growth in the cultures when the cell concentration is 50,000 cells per cc. The temperature is controlled by a mercury thermoregulator, the air being circulated by an electric fan.

Experimental results.—*The absorption of nitrate.*—In order to determine the effect of the concentration of phosphate in the medium on the rate of absorption of nitrate, experiments were performed in the following way: cells from a stock culture which had been grown in the light of a north window for six days were placed in fresh sea water, and the cell concentration was adjusted to 50,000 cells per cc. The suspension was enriched with nitrate and then divided in flasks. Different amounts of phosphate were added to each flask. The cultures were placed in the dark for twelve hours and were then placed in the light at a temperature of 16°C. The rate of absorption was determined by the difference between the nitrate present when the cultures were placed in the light and the final concentration of nitrate in the medium. Any differences in the rate of absorption of nitrate under these conditions may be attributed to the different phosphate concentrations, since all other variables are controlled.

The results of three experiments performed in this way at different nitrate concentrations are presented in table 1. In each experiment the phosphate concentration varies between less than ten and about one hundred gamma per liter. The data show that this tenfold increase in the concentration of phosphate has no influence on the rate of absorption of nitrate from the medium.

Since these experiments were performed at three different nitrate concentrations they show the effect of the concentration of nitrate on the rate of its absorption. The cells suspended in the medium containing about 240 gamma of nitrate nitrogen per liter absorbed two and one-half times as much nitrogen as those in the medium containing only fifty gamma per liter.

In order to study in more detail the relation between the concentration of nitrate in the medium and the rate of absorption of nitrate, experiments were performed in which the nitrate concentration was different in the various cultures. Although the phosphate concentration in these cultures was not equal, the data presented in table 1 show that this does not affect the rate of nitrate absorption. The results are summarized in table 2, where they are arranged according to the original concentration of nitrate in the medium. The rate of absorption increases steadily with the increase in the concentration of nitrate in the medium. In figure 1 the relation between the average concentration of nitrate in the medium and the rate of absorption of nitrate by the cells is shown. The data from tables 1 and 2

Table 1. *The absorption of nitrate by illuminated cultures of Nitzschia Closterium at 16°C. The original cell concentration was adjusted in all cases to 50,000 cells per cc.*

Original phosphate gamma/L.	Original nitrate gamma N/L.	Final nitrate gamma N/L.	Nitrate absorbed gamma N/L.	Time hours	Nitrate absorbed per cell per hour gamma
<10	47	5	42	12	7.0, 10^{-8}
94	50	7	43	12	7.2 "
<10	147	70	77	12	12.8 "
15	108	72	36	5.8	12.4 "
22	150	114	36	5.8	12.4 "
105	127	46	81	12	13.5 "
<10	247	133	114	12	19.0 "
94	236	137	99	12	16.5 "

TABLE 2. *The absorption of nitrate by illuminated cultures of Nitzschia Closterium at 16°C. in relation to the concentration of nitrate in the medium. The cell concentration was adjusted in all cases to 50,000 cells per cc.*

Original nitrate gamme N/L.	Final nitrate gamma N/L.	Average nitrate gamma N/L.	Nitrate absorbed gamma N/L.	Time hours	Nitrate absorbed per cell per hour gamma
63	32	47	31	5.8	10.7, 10^{-8}
97	24	60	73	12.0	12.1 "
100	62	81	38	5.8	13.1 "
128	38	83	90	12.0	14.9 "
183	108	145	75	11.5	13.0 "
187	94	140	93	12.0	15.5 "
200	112	156	88	12.0	14.6 "
270	165	217	105	12.0	17.5 "
300	241	270	59	5.8	20.3 "
319	219	269	100	12.0	16.7 "
326	241	284	85	10.5	16.2 "

are included in this figure. Although the experimental variation is large at the high concentrations of nitrate, since these must be measured by dilution, the increasing rate of absorption with increasing concentration is plainly demonstrated. Above a concentration of about 200 gamma nitrate nitrogen per liter the rate of absorption of nitrate appears to approach a limiting value.

These experiments show that although the rate of absorption of nitrate is independent of the concentration of phosphate, it is directly related to the concentration of nitrate in the medium.

The absorption of phosphate.—In the utilization of phosphate by diatoms two types of absorption can be distinguished. Absorption from the medium always occurs when the cells are grown in the light, provided phosphate is available. Phosphate is also absorbed in the dark by cells which are deficient in phosphorus, as described in another paper (Ketchum, 1939). Since this effect is so pronounced, it is necessary to be certain that it is not confusing the results obtained in the study of the absorption by illuminated cultures. It was found that stock cultures should be no more than five or six days old when used. Cells from such a culture are resuspended in fresh sea water and placed in the dark for a period of twelve or more hours. By this time the "phosphate debt" is satisfied. The cultures are then placed in the light, and the absorption of phosphate from the medium may be measured.

Experiments were performed on cells prepared in this way to determine the influence of the phosphate concentration in the medium on the rate of absorption of phosphate. The cultures were divided in flasks which were placed in the light at 16°C. after the addition of a different amount of phosphate to each flask. The phosphate concentration was measured when they were placed in the light, and the rate of absorption was determined by the difference between this and the final concentration of phosphate in each case.

The results of three experiments performed in this way at three different nitrate concentrations are presented in table 3 and figure 2. In each ex-

TABLE 3. *The rate of absorption of phosphate by illuminated cultures of Nitzschia Closterium at 16°C. in relation to the concentration of phosphate in the medium at three different nitrate concentrations.*

Original nitrate gamma N/L.	Original phosphate gamma/L.	Final phosphate gamma/L.	Phosphate absorbed gamma/L.	Time hours	Initial count cells/L.	Phosphate absorbed per cell per hour gamma
0–5	45	32	13	6	230, 10^{6}	0.94, 10^{-8}
0–5	70	52	18	6	"	1.30 "
0–5	104	82	22	6	"	1.60 "
0–5	188	163	25	6	"	1.81 "
65	92	45	47	13.5	60, 10^{6}	5.8, 10^{-8}
65	132	77	55	13.5	"	6.8 "
69	167	104	63	13.5	"	7.8 "
63	264	199	65	13.5	"	8.0 "
220	11	6	5	6	50, 10^{6}	1.7, 10^{-8}
220	43	19	24	6	"	8.0 "
220	94	64	30	6	"	10.0 "
220	253	220	33	6	"	11.0 "

periment the rate of absorption of phosphate increases with an increase in the phosphate concentration in the medium. The rate of absorption of phosphate also depends on the concentration of nitrate in the medium, as comparison of the results obtained at the three different nitrate concentrations shows.

The experiment in which the cultures contained no nitrate is particularly interesting. Since nitrate-free sea water is difficult to obtain, a culture was allowed to grow until no nitrate could be detected in the medium by the reduced strychnine method. It was then divided in four flasks and a different amount of phosphate added to each flask. After six hours in the light a definite absorption of phosphate was measured, showing a dependence of the rate of absorption on the phosphate concentration which is similar to that demonstrated by the other two experiments. From this experiment it is clear that the cells are able to absorb phosphate from the medium, even when no measurable nitrate is present. Comparison with the other two experiments, however, shows that the presence of nitrate materially increases the rate of absorption of phosphate.

Experiments were also performed to study the effect of the concentration of nitrate on the rate of absorption of phosphate from the medium. In each of these experiments the original concentration of phosphate was equal, whereas the concentration of nitrate was different in the various flasks. The amount of phosphate absorbed by the cells was determined by the difference between the initial concentration of phosphate and the concentration after a period of illumination at 16°C. The results of five experiments performed in this way are presented in table 4 and figure 3, where the values plotted for the zero concentration of nitrate are taken from the experiment reported in figure 2. Again a family of curves is obtained which shows the dependence of the rate of absorption of phosphate on the concentrations of both phosphate and nitrate. Each curve of the family was obtained for a different concentration of phosphate, which is given by the figure at the end of the curve. All the curves show a relation between the rate of absorption of phosphate and the nitrate concentration. Intercomparison of the curves shows that, for a given concentration of nitrate, the rate of absorption of phosphate increases with increasing concentrations of phosphate.

The rate of growth under the experimental conditions used.—It was possible that the various experimental conditions used might influence the rate

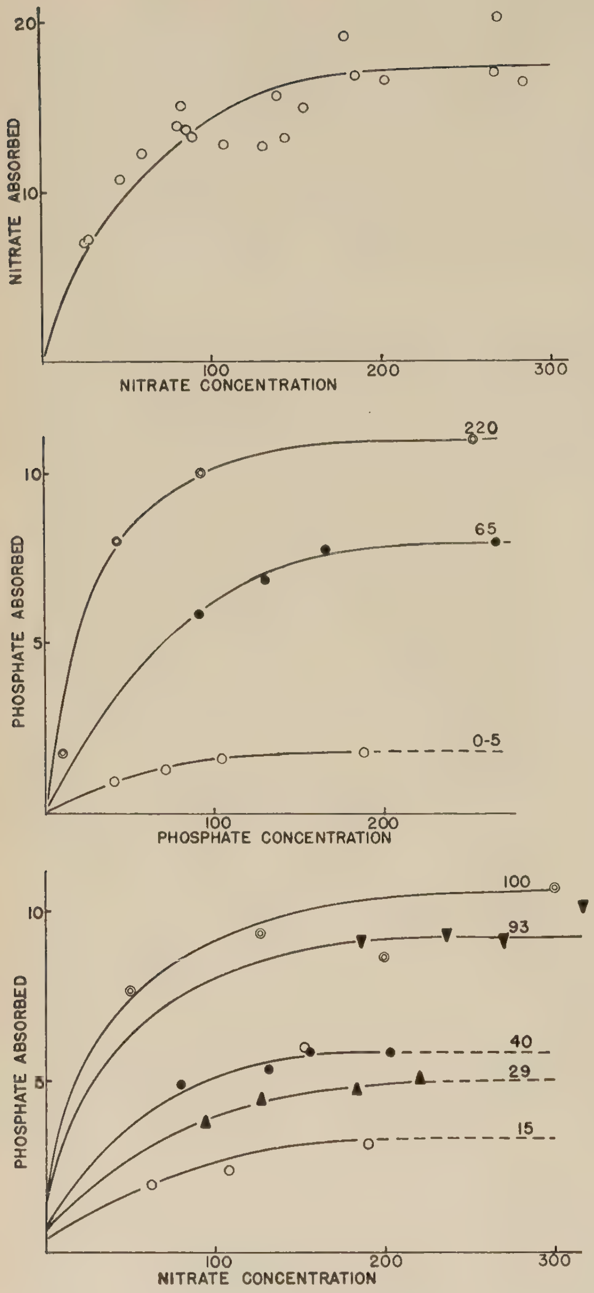


Fig. 1–3.—Fig. 1. The relation between the rate of absorption of nitrate by illuminated cultures of *Nitzschia Closterium* and the concentration of nitrate in the medium. Abscissa, concentration of nitrate in the medium, units gamma N per liter. Ordinate, nitrate absorbed per cell per hour, units gamma N×10^8.—Fig. 2. Relation between the rate of absorption of phosphate by illuminated cultures of *Nitzschia Closterium* at 16°C. and the concentration of phosphate in the medium, at three different concentrations of nitrate. The figure at the end of each curve shows the nitrate concentration for that experiment; units—gamma N per liter. Ordinate, phosphate absorbed per cell per hour, units gamma $PO_4 \times 10^8$. Abscissa, concentration of phosphate in the medium, units gamma PO_4 per liter.—Fig. 3. Relation between the rate of absorption of phosphate by illuminated cultures of *Nitzschia Closterium* at 16°C. and the concentration of nitrate in the medium at five different phosphate concentrations. The figure at the end of each curve shows the phosphate concentration at which that experiment was performed, units gamma per liter. Ordinate, phosphate absorbed per cell per hour, units gamma $PO_4 \times 10^8$. Abscissa, concentration of nitrate in the medium, units gamma N per liter.

Table 4. *The rate of absorption of phosphate by illuminated cultures of Nitzschia Closterium at 16°C. in relation to the concentration of nitrate in the medium at various phosphate concentrations.*

Original nitrate gamma N/L.	Original phosphate gamma/L.	Final phosphate gamma/L.	Phosphate absorbed gamma/L.	Time hours	Initial count cells/L.	Phosphate absorbed per cell per hour gamma
63	15	10	5	5	50, 10^6	2.0, 10^{-8}
108	15	9	6	5	"	2.4 "
154	15	0	15	5	"	6.0 "
190	15	7	8	5	"	3.2 "
94	29	8	21	11.5	50, 10^6	3.7, 10^{-8}
128	29	4	25	11.5	"	4.4 "
183	29	2	27	11.5	"	4.8 "
222	29	0	29	11.5	"	5.0 "
80	40	29	11	4.5	50, 10^6	4.9, 10^{-8}
131	40	28	12	4.5	"	5.3 "
156	40	27	13	4.5	"	5.8 "
204	40	27	13	4.5	"	5.8 "
186	93	38	55	12.0	50, 10^6	9.2, 10^{-8}
236	93	37	56	12.0	"	9.4 "
270	93	38	55	12.0	"	9.2 "
319	93	32	61	12.0	"	10.2 "
50	100	45	55	12.0	60, 10^6	7.7, 10^{-8}
127	100	32	68	12.0	"	9.4 "
202	100	38	62	12.0	"	8.7 "
300	100	68	32	5.0	"	10.6 "

of growth of the cells and thus indirectly control the rate of absorption of phosphate and nitrate. Experiments were therefore performed to discover what effect the concentrations of nitrate and phosphate in the medium have upon the rate of growth. These experiments were done in the same way as those reported above, except that they were grown in the light of a north window instead of in the artificially illuminated air bath. Longer periods of time were used in these experiments in order to obtain significant differences in the cell counts. A direct measure of the rate of growth is given by the division rate per cell (k), which is defined by the equation $k=1/t\,[\ln C_t/C_o]$ in which C_t and C_o are the cell counts at the end and beginning of time t.

The results of the experiments are summarized in table 5. In the first experiment the effect of the nitrate concentration on the rate of growth was studied. All these cultures were started with an equal phosphate concentration, and the nitrate concentration varied from 47 to 525 gamma per liter.

Table 5. *The growth of cultures of Nitzschia Closterium in media containing various nitrate and phosphate concentrations. Grown in the light of a north window at room temperature.*

Expt. no.	Initial phosphate gamma/L.	Initial nitrate gamma N/L.	Initial count cells/L.	Final count cells/L.	Time hours	Division rate (k) Days^{-1}
1	50	47	46.0, 10^6	170, 10^6	45	0.70
	50	185	47.0 "	170 "	45	0.68
	50	375	49.0 "	180 "	45	0.69
	50	525	44.0 "	170 "	45	0.72
2	15	500	16.7 "	26.7 "	36	0.31
	30	500	16.7 "	38.8 "	36	0.56
	50	500	16.7 "	45.1 "	36	0.67
	70	500	16.7 "	47.6 "	36	0.70
	110	500	16.7 "	45.6 "	36	0.68
3	54	500	44.4 "	170 "	45	0.72
	105	500	46.0 "	160 "	45	0.67
	145	500	47.0 "	170 "	45	0.69
4	52	150	46.0 "	180 "	48	0.68
	103	150	50.0 "	180 "	48	0.64
	153	150	47.0 "	190 "	48	0.70

All the experiments on the absorption of nitrate from the medium were performed within this range of concentrations. The rate of growth in all these flasks was nearly constant in spite of this tenfold increase in the concentration of nitrate.

The second, third, and fourth experiments reported in table 5 relate the rate of growth with the concentration of phosphate in the medium. They show that between 50 and 150 gamma of phosphate per liter the rate of growth is independent of the phosphate concentration. Below a concentration of 50 gamma of phosphate per liter, however, the rate of growth is limited by the concentration of phosphate in the medium.

Since the rate of growth is constant at different concentrations of phosphate and nitrate, the differences in the rate at which these ions are absorbed is not due to different growth rates. Concentrations of phosphate below 50 gamma per liter, however, may limit the rate of absorption of phosphate indirectly by affecting the rate of growth. It is interesting to note that such low concentrations of phosphate have no influence on the rate of absorption of nitrate (see table 1). It appears, therefore, that in these experiments the effect of the rate of growth is negligible in comparison with the direct effect of the concentration of the nutrients on the rate of absorption.

TABLE 6. *The proportions in which phosphate and nitrate are absorbed from media containing various concentrations of these ions as predicted from data presented in tables 1, 2, 3, and 4 and in figures 1, 2, and 3.*

Phosphate conc. Gamma/L.	Nitrate conc. gamma N/L.	PO_4 abs. /cell/hour gamma$\times 10^8$	NO_3 abs. /cell/hour gamma$\times 10^8$	Conc. ratio PO_4:N grams:grams	Abs. ratio ΔPO_4:ΔN grams:grams	Abs. ratio ΔP:ΔN atoms:atoms
15	10	0.7	3.1	1.5	0.23	0.034
15	20	1.0	5.4	0.75	0.18	0.027
15	50	1.6	9.4	0.30	0.17	0.025
15	100	2.4	13.8	0.15	0.17	0.025
15	200	3.2	17.0	0.075	0.19	0.028
15	300	3.2	17.2	0.05	0.19	0.028
30	10	1.2	3.1	3.0	0.39	0.057
30	20	1.6	5.4	1.5	0.30	0.044
30	50	2.8	9.4	0.6	0.30	0.044
30	100	4.0	13.8	0.3	0.29	0.043
30	200	5.0	17.0	0.15	0.29	0.043
30	300	5.1	17.2	0.10	0.30	0.044
40	10	1.7	3.1	4.0	0.55	0.081
40	20	2.2	5.4	2.0	0.41	0.060
40	50	3.6	9.4	0.8	0.38	0.056
40	100	5.1	13.8	0.4	0.37	0.055
40	200	5.9	17.0	0.2	0.35	0.052
40	300	5.9	17.2	0.13	0.34	0.050
65	10	1.8	3.1	6.5	0.58	0.085
65	20	2.6	5.4	3.25	0.48	0.071
65	50	4.2	9.4	1.30	0.45	0.066
65	100	6.3	13.8	0.65	0.45	0.066
65	200	7.5	17.0	0.33	0.44	0.065
65	300	7.5	17.2	0.22	0.44	0.065
90	10	3.0	3.1	9.0	0.97	0.143
90	20	4.6	5.4	4.5	0.85	0.124
90	50	5.8	9.4	1.8	0.62	0.091
90	100	7.8	13.8	0.9	0.57	0.084
90	200	9.4	17.0	0.45	0.55	0.081
90	300	9.4	17.2	0.3	0.55	0.083
200	10	3.2	3.1	20.0	1.03	0.152
200	20	4.9	5.4	10.0	0.91	0.134
200	50	6.6	9.4	4.0	0.70	0.103
200	100	9.1	13.8	2.0	0.66	0.097
200	200	10.0	17.0	1.0	0.59	0.087
200	300	10.1	17.2	0.65	0.59	0.087
300	10	3.5	3.1	30.0	1.13	0.167
300	20	5.0	5.4	15.0	0.92	0.135
300	50	6.8	9.4	6.0	0.72	0.106
300	100	9.2	13.8	3.0	0.67	0.099
300	200	11.0	17.0	1.5	0.65	0.096
300	300	11.0	17.2	1.0	0.64	0.095

Since the rate of absorption of phosphate and nitrate was measured on illuminated cultures, cell division must have taken place. The growth rates recorded in table 5 indicate that the cells would almost double in number in the eight to ten hours of continuous illumination allowed for these experiments. The rates of absorption have been expressed in terms of the initial number of cells in the culture. No correction for the amount of growth has been made. Expressed in this way the results are comparable for all experiments except those containing less than 50 gamma of phosphate per liter, where lower rates of growth are observed.

Ratio of absorption.—From the data concerning the rate of absorption of phosphate and nitrate from media of various compositions it is possible to predict the ratio in which these ions will be absorbed from media in which they occur in any proportion. The ratio in which phosphate and nitrate are absorbed at seven phosphate and six nitrate concentrations have been calculated, using the rates of absorption obtained from figures 1, 2, and 3. These are presented in table 6, where they are grouped according to the phosphate concentration, each group containing the data for six nitrate concentrations. The ratio of absorption, $\Delta P:\Delta N$, is constant in each group, even though the nitrate concentration varies between 10 and 300. It will be remembered that the rate of absorption of both nitrate and phosphate are dependent upon the nitrate concentration. The effect of the nitrate upon the absorption of these two ions must be similar or the constant ratio would not be obtained. This similarity is not found at low nitrate concentrations, since these limit the rate of absorption of nitrate to a greater extent than the rate of absorption of phosphate. An increase in the value for the ratio of absorption is observed for these low nitrate concentrations.

Intercomparison of the groups shows that the value for the ratio increases with increasing concentrations of phosphate.

In the fifth column of the table the ratio in which phosphate and nitrate are present in the medium is shown. For each phosphate concentration these vary thirtyfold, since the nitrate concentration varies between 10 and 300. Comparison of these figures with the ratio of absorption shows that the latter is completely independent of the proportions of nitrate to phosphate in the medium.

Under normal conditions of growth both phosphate and nitrate are being continuously removed from the medium. Since the concentration of phosphate in the medium determines the ratio in which these ions are absorbed, this ratio must constantly change while the cells are growing. In figure 4 the changes in the medium during constant growth of the cells are presented. The light lines show the changes in the medium predicted from the data in table 6. Simultaneous measurements of the phosphate and nitrate remaining in the medium after various periods of illumination were made on a number of cultures. These data are included in figure 4, where the points represent the composition of the medium at various times. The heavy lines connecting these points show how the growth of the cells changes the composition of the medium. The changes observed in these cultures agree closely with the predicted changes in the medium.

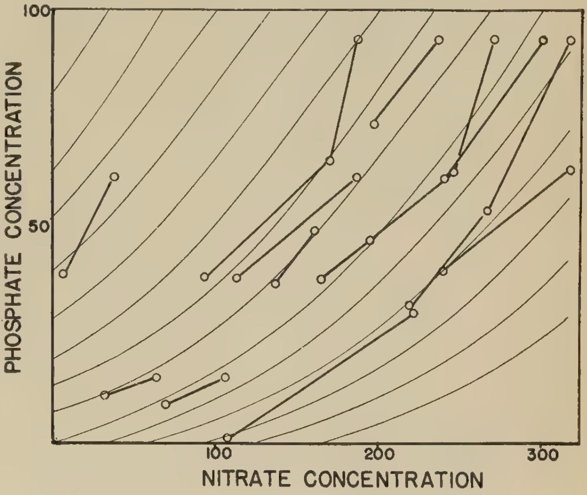


Fig. 4. The simultaneous removal of phosphate and nitrate from sea water of various compositions. The light lines show the changes predicted in table 6 from the data on the rate of absorption. The points, connected with heavy lines, show the changes observed when simultaneous measurements of phosphate and nitrate concentrations are made on actively growing cultures. Ordinate concentration of nitrate in the medium, units gamma N per liter. Abscissa concentration of phosphate in the medium, units gamma PO_4 per liter.

The usual ratio of phosphate phosphorus to nitrate nitrogen in the sea would be represented in figure 4 by a line drawn from the origin through the medium containing 298 gamma of nitrate nitrogen and 100 gamma of phosphate (PO_4). It is apparent that this line does not coincide with the way in which phosphate and nitrate are absorbed by the cells. If the ratio P:N in the medium is high, the metabolism of the cells brings the ratio closer to the usual one; if the ratio is low, the metabolism of the cells increases the original departure from the usual ratio.

Discussion.—Schreiber (1928) and Braarud and Foyn (1931) found that the growth of unicellular algae is limited by low concentrations of phosphate and nitrate, respectively. In their experiments the concentrations of the nutrients studied was low, and they were undoubtedly exhausted before the end of the experiments. Such experiments certainly show that a deficiency of an essential element reduces the total crop which can be produced in a given medium, but no conclusions can be drawn concerning the rate of growth at a given concentration. Barker (1935b) showed that the rate of growth of marine dinoflagellates is independent of the concentration of nitrate in the medium. The concentrations used in his work were sufficiently high so that they were not exhausted. The data presented in this paper confirm Barker's conclusions, since the rate of growth of *Nitzschia Closterium* is independent of the concentration of nitrate and phosphate over the concentration range of natural sea water.

It has been commonly assumed that low concentrations of a nutrient in natural waters limit the rate of growth and the rate of absorption of the nutrient simultaneously. The data presented in this paper show that this is not always true. The rate of absorption of both phosphate and nitrate varies in media containing different concentrations of these ions, even though the rate of growth is independent of their concentrations.

The data concerning the proportions in which nitrate and phosphate are absorbed indicate that at least two synthetic processes involving phosphorus are taking place and that these reactions are rigorously controlled by the concentration of both phosphate and nitrate in the medium. One of these reactions apparently involves both nitrogen and phosphorus metabolism and is controlled by the concentration of nitrate in the medium. It will be remembered that regardless of the concentration of nitrate in the medium the proportion in which phosphate and nitrate are absorbed is constant for a given phosphate concentration. Since the different nitrate concentrations influence the rate of absorption of both phosphate and nitrate, these rates must increase in direct proportion, as though a compound containing both nitrogen and phosphorus were being synthesized.

Phosphorus must also be utilized in reactions which do not involve nitrogen. The rate at which these reactions proceed must be dependent on the concentration of phosphate in the medium, since increased concentrations of phosphate increase the rate of absorption of phosphate with no influence on the rate of absorption of nitrate.

The various reactions involving phosphorus can be most readily studied in unicellular forms, since the rates at which they proceed can be so easily controlled. This study is being extended to the formation of various organic compounds of phosphorus under the conditions discussed in this paper.

SUMMARY

The rate of absorption of nitrate by the marine diatom, *Nitzschia Closterium,* is independent of the concentration of phosphate in the medium, but it increases as the concentration of nitrate in the medium increases.

The rate of absorption of phosphate is directly dependent on the concentration of both phosphate and nitrate in the medium.

The rate of growth is independent of the concentrations of phosphate and nitrate in the medium except for phosphate concentrations of less than 50 gamma per liter, when it decreases.

The ratio in which phosphate and nitrate are absorbed is constant for each concentration of phosphate in the medium, regardless of the concentration of nitrate, except that at very low concentrations of nitrate the ratio of absorption increases.

The ratio of absorption $\Delta P:\Delta N$ increases as the concentration of phosphate in the medium increases.

The normal course of absorption in cultures does not directly correspond to the usual ratio found in sea water. If the cells are in a medium in which the ratio of concentrations is somewhat higher than usual, the absorption by the cells tends to reduce the ratio toward the usual value. If the ratio of concentrations is lower than usual, the metabolism tends to increase the discrepancy.

Biological Laboratories,
Harvard University, and
Woods Hole Oceanographic Institution

LITERATURE CITED

Atkins, W. R. G. 1923. Phosphate content of fresh and salt waters in its relationship to the growth of the algal plankton. Jour. Mar. Biol. Assn. N. S. 13: 119–150.

———. 1926a. Quantitative consideration of some factors concerned in plant growth. 2. Some chemical factors. Jour. Cons. Int. Explor. Mer. 1: 197–226.

———. 1926b. Phosphate content of sea water in relation to growth of algal plankton. Jour. Mar. Biol. Assn. N. S. 14: 447–467.

Barker, H. A. 1935a. Photosynthesis in diatoms. Arch. Mikrobiol. 6: 141–156.

———. 1935b. The culture and physiology of the marine dinoflagellates. Arch. Mikrobiol. 6: 157–181.

Braarud, T., and B. Foyn. 1931. Beitrage zur Kenntnis des Stoffweschsel im Meere. Avhandl. Norske Videnskab. Akad. i Oslo. I Mat. Nat. Kl. 14: 1–24.

Brandt, K. 1899. Ueber der Stoffwechsel im Meere. Wiss. Meeresuntersuch. Abt. Kiel 4: 213–230.

———. 1902. Ueber der Stoffwechsel im Meere. Wiss. Meeresuntersuch. Abt. Kiel 6: 23–79.

Cooper, L. H. N. 1933. Chemical constituents of biological importance in the English Channel. Jour. Mar. Biol. Assn. N. S. 18: 677–729.

———. 1937. On the ratio of nitrogen to phosphorus in the sea. Jour. Mar. Biol. Assn. N. S. 22: 177–182.

Harvey, H. W. 1926. Nitrate in the sea. I. A method for estimating nitrates in sea water. Jour. Mar. Biol. Assn. N. S. 14: 71–88.

———. 1928. Nitrate in the sea. II. Jour. Mar. Biol. Assn. N. S. 15: 183–190.

———, L. H. N. Cooper, M. V. Lebour, and F. S. Russell. 1935. Plankton production and its control. Jour. Mar. Biol. Assn. 20: 407–442.

Ketchum, B. H. 1939. The development and restoration of deficiencies in the phosphorus and nitrogen composition of unicellular plants. Jour. Cell. and Comp. Physiol. 13: (in press).

———, and A. C. Redfield. 1938. A method for maintaining a continuous supply of marine diatoms by culture. Biol. Bull. 75: 165–169.

Kreps, E., and N. Verjbinskaya. 1932. Consumption of nutrient salts in the Barents Sea. Jour. Cons. Int. Explor. Mer. 7: 25–46.

Marshall, S. M., and A. P. Orr. 1928. Photosynthesis of diatom cultures in the sea. Jour. Mar. Biol. Assn. N. S. 15: 321–360.

Redfield, A. C. 1934. On the proportions of organic derivatives in sea water and their relation to the composition of plankton. James Johnstone Memorial Volume, Liverpool, pp. 176–192.

———, H. P. Smith, and B. H. Ketchum. 1937. The cycle of organic phosphorus in the Gulf of Maine. Biol. Bull. 73: 421–442.

Reuszer, H. W. 1933. Marine bacteria and their rôle in the cycle of life in the sea. III. The distribution of bacteria in the ocean waters and muds about Cape Cod. Biol. Bull. 65: 480–497.

Schreiber, E. 1928. Die Reinkultur von Marimen Phytoplankton und deren Bedeutung für die Erforschung der Production-fahigkeit des Meereswasser. Wiessen. Meeresuntersuch. abt. Helgoland. 16: No. 10, 1–34.

Wattenberg, H. 1937. Critical review of the methods used for determining nutrient salts and related constituents in salt water. Rapp. Proc. Verb. Cons. Int. Explor. Mer. ciii: 5–25.

Contribution No. 217

SOME APPLICATIONS OF STATISTICAL METHODS TO PROBLEMS IN MODERN PHYSICAL OCEANOGRAPHY*

By

H. R. SEIWELL

---

*Contribution No.217 from the Woods Hole Oceanographic Institute.

INTRODUCTION

Descriptions of geophysical observations intended to serve as basis for theoretical explanations must give adequate accounts of space and time variability. Frequently, however, the data of such investigations do not readily lend themselves to analysis by the usual formal methods of mathematical statistics, and, in particular, is this true of observations on the physical structure and circulation of the oceans. In the ocean basins simultaneous observations at more than one point, or even long continued observations along a single vertical, have not been possible, and as a result, in absence of information on time variability, certain not completely justified assumptions of average conditions have been made when developing pictures of space distributions of oceanographic elements. However, in certain instances, specific information may be brought out by the application of formal methods as is illustrated by the following, in which three types of modern physical oceanographical problems are treated.

Correlation between Salinity and Oxygen content in the western North Atlantic

At mid depths of the western North Atlantic ocean certain relationships exist between salt and oxygen contents of the water masses; as, for instance, in the approximate central part of this basin (between latitudes 25°N and 35°N) where both salinity and minimum oxygen concentration decrease horizontally westward toward the Gulf Stream; a fact which suggests (from oceanographic information) that the presence of Mediterranean water in the North Atlantic raises the concentration of its minimum oxygen concentration.

Graphical representation of minimum oxygen concentration (O_2) as a function of salinity anomaly (D) between latitudes 35° and 25°N in the western North Atlantic basin (Fig. 1) suggests an approximate straight line relationship. The number of observations is not large, but approximation to normality is indicated by the majority of points clustering about the central part of the scatter diagram. Standard deviations of oxygen values, σ_{O_2} , and D values, σ_D, are:

$$\sigma_{O_2} = 0.178$$

$$\sigma_D = 4.06$$

And, on the assumption that conditions for existence of a significant correlation coefficient are fulfilled, the Pearsonian coefficient, r , was calculated to be:

$$r = 0.782$$

indicating a high correlation to exist between minimum oxygen values and salinity anomalies in this strip of water.

The actual correlation coefficient in this case differs from zero, so the distribution of calculated values of r (which depends on the actual value of the coefficient and on the size of the sample) will be decidedly non normal (since the number of pairs of values is small), and the chances are in favor of drawing a sample from the population in which the calculated value of r will be greater than the actual value. To examine the probability that the actual value of r differs significantly from the calculated value (r = 0.782) use is made of the practically normal function

$$Z' = \frac{1}{2} \ln \frac{1 + r}{1 - r}$$

having a standard deviation:

$$\sigma_{Z'} = \frac{1}{\sqrt{N-3}}$$

when,N,is the number of pairs of values (36). Thus, testing the possibility that the actual correlation coefficient for the above data may be 0.600 instead of 0.782 we have:

$$Z_1' = \frac{1}{2} \ln \frac{1 + 0.600}{1 - 0.600} = .69315$$

and

$$Z_2' = \frac{1}{2} \ln \frac{1 + 0.782}{1 - 0.782} = 1.05076$$

and the standard deviation of Z' :

$$\sigma_Z = \frac{1}{\sqrt{36 - 3}} = 0.17409$$

The ratio of the difference, $Z_2' - Z_1'$, to the standard deviation:

$$\frac{1.05076 - .69315}{0.17409} = 2.0542$$

is more than two times the standard deviation showing it to be very unlikely that the actual value of this coefficient is as low as 0.600.

Normal Frequency Distribution of the Density of Sea Water at Depth of the Observed Minimum Oxygen Concentration

Oceanographic data from the North Atlantic ocean have shown that the density surface along which dissolved atmospheric oxygen was observed to attain its principle minimum concentration lay between 1.02695 and 1.02741 ($\sigma_t = 26.95 - 27.41$), a range which likely has no physical significance and probably results from a combination of causes associated with the sampling methods in use; in which case the observed values should be distributed normally about the most probable density value. To test this hypothesis a histogram of the frequency distribution of density (σ_t) values associated with the observed minimum oxygen concentration is approximated by a normal curve and the goodness of fit tested.

Density (σ_t) values associated with the observed minimum oxygen values were grouped into cells having a class interval of 0.04 units of σ_t giving the frequency distribution in Table 1 , the general form of which suggests that the data are normal. Referring to class marks (0, 1, 2,.......n) the first four moments calculated about the mean (6.311) are:

$$M_0 = 135.000$$

$$M_1 = 0.000$$

$$M_2 = 1{,}088.966$$

$$M_3 = -264.035$$

$$M_4 = 18{,}545.557$$

TABLE 1

Class interval	Class Marks	Frequency	Graduated Frequency
26.93 - 26.96	0	1	1.6
26.97 - 27.00	1	4	3.3
27.01 - 27.04	2	10	6.0
27.05 - 27.08	3	12	10.0
27.09 - 27.12	4	13	13.6
27.13 - 27.16	5	13	17.1
27.17 - 27.20	6	14	19.0
27.21 - 27.24	7	18	18.5
27.25 - 27.28	8	17	15.9
27.29 - 27.32	9	12	12.1
27.33 - 27.36	10	12	8.1
27.37 - 27.40	11	7	4.8
27.41 - 27.44	12	2	2.5

Applying Sheppard's adjustments to correct for the error in assuming that all frequencies in the class intervals were concentrated at the mean value, the adjusted moments become:

$$M_0 = 135.000$$

$$M_1 = 0.000$$

$$M_2 = 1{,}077.716$$

$$M_3 = -264.035$$

$$M_4 = 18{,}005.011$$

from which the following fundamental statistics are calculated. Thus, the standard deviation(1), σ , of the distribution is:

$$\sigma = \sqrt{\frac{\mu_2}{\mu_0}} = 2.825$$

---

(1) This is standard deviation of the distribution referred to the above class marks, the standard deviation when referred to the mid class density values (Table 1) is: $\sigma = 0.11301$

the skewness, S:

$$S = \frac{\mu_3}{2\mu_0\sigma^3} = -0.04336$$

and its probable error:

$$\text{P.E. in skewness} = \frac{.8261}{\sqrt{\mu_0}} = 0.0711$$

the value of β_2 comes out to be:

$$\beta_2 = \frac{\mu_4}{\mu_0\sigma^4} = 2.093$$

and its probable error:

$$\text{P.E. in } \beta_2 = \frac{3.3044}{\sqrt{\mu_0}} = 0.285$$

The two latter statistics (skewness and β_2) are fundamental for decision as to the normality of the data, and since both are influenced by random sampling, departures of skewness from 0 and of β_2 from 3 does not necessarily indicate that the distribution is non normal. As a general rule if skewness exceeds three times its probable error, and if β_2 differs from 3 by more than three times its probable error the distribution may be considered as being non normal.

Thus, for the case under consideration the skewness is less than its probable error and the excess or Kurtosis

$$\left|\beta_2 - 3\right| = 0.907$$

which exceeds three times its probable error by 0.052, but for practical purposes the distribution is taken as being normal. The equation of the normal frequency curve fitting the distribution is:

$$y = 47.788 \frac{e^{-\frac{1}{2}\left(\frac{X - 6.311}{2.825}\right)^2}}{\sqrt{2\pi}}$$

and is superimposed on the histogram of the observed frequency distribution in Fig. 2. Theoretical frequencies obtained from this curve are given in Table 1, and calculation of the Chi squared function, where:

$$\chi^2 = \frac{(F_1 - f_1)^2}{F_1} + \frac{(F_2 - f_2)^2}{F_2} + - - - - + \frac{(F_n - f_n)^2}{F_n}$$

(F being the theoretical, or graduated frequency, and f the observed frequency) gives:

$$\chi^2 = 7.9969$$

For this calculation, frequencies at the tails of the curve, less than 7, were clubbed together leaving 11 groups, and since three constants have been fitted (total, mean, and standard deviation) 8 (n) degrees of freedom remain. Thus, entering Elderton's table at n' = 9 (n' = n+1) the value of the Pearson probability is:

$$P = 0.43$$

from which it may be concluded that in 43 times out of 100 we should get in random sampling a fit as bad or worse if the real distribution was normal.

The mode, M_o or most probable value of σ_t at the minimum oxygen concentration in the western North Atlantic is interpreted to be:

$$M_o = L + \frac{C \cdot F}{F + f}$$

(where L is the lower limit of the modal class; C, the class interval; F, the frequency of the class above the mode; and, f , the frequency of the class just below the mode), thus:

$$M_o = 27.232 \neq 0.008$$

And, since three times the probable error is not likely to be exceeded, the limits of density (σ_t) level for the occurrence of the minimum oxygen value in the western North Atlantic is, tentatively,

$$\sigma_t = 27.207 \quad \text{to} \quad 27.257$$

This result was later tested by selecting, at random, a locality in the western North Atlantic (Station 2639: 66° 25'W, 35° 07'N) and sampling the water column at intervals separated by approximately 1/20 of the customary vertical distance, the results given in Table 2 show the observed density to agree with the theoretical value of 27.232 ± 0.008.

TABLE 2

Meters Depth	Density σ_t	Oxygen $cm\ L^{-1}$
803	27.09	3.35
820	27.14	3.32
836	27.16	3.30
853	27.23	3.30
870	27.26	3.30
894	27.27	3.32
918	27.33	3.44

A similar calculation based on density distribution at the observed depth of the oxygen minimum concentration in the Caribbean Sea has been carried out in identically the same way. The values which ranged between $\sigma_t = 26.85$ to $\sigma_t = 27.44$ were grouped into cells having a class interval of 0.04 units of σ_t (Table 3). Referring the frequency distribution to the same class marks as before the adjusted moments were calculated:

$$M_o = 147.000$$

$$M_1 = 0.000$$

$$M_2 = 650.686$$

$$M_3 = 40.4281$$

$$M_4 = 8431.0788$$

The following statistics characterize the distribution:

Standard deviation,(2) $\sigma = 2.1039$

---

(2) This is standard deviation of the distribution referred to the above class marks, the standard deviation when referred to mid class density values (Table 3) is $\sigma = 0.10520$

Skewness, S = 0.01476

Probable error in skewness = 0.0681,

$$\beta_2 = 2.9273$$

and

Probable error in β_2 = 0.2725.

TABLE 3

Class interval	Class Marks	Frequency	Graduated Frequency
26.85 - 26.89	0	1	0.5
26.90 - 26.94	1	2	1.6
26.95 - 26.99	2	4	4.5
27.00 - 27.04	3	7	9.9
27.05 - 27.09	4	18	17.6
27.10 - 27.14	5	30	24.8
27.15 - 27.19	6	30	27.9
27.20 - 27.24	7	21	25.0
27.25 - 27.29	8	12	17.9
27.30 - 27.34	9	13	10.2
27.35 - 27.39	10	7	4.7
27.40 - 27.44	11	2	1.7

The value of skewness is well within its probable error as is also the value $|\beta_2 - 3|$ = 0.0727, indicating the distribution to be normal. The equation of the normal frequency curve fitting the distribution(3) is:

$$y = 69.8702 \frac{e^{-\frac{1}{2}\left(\frac{X - 6.0204}{2.1039}\right)^2}}{\sqrt{2\pi}}$$

---

(3) Average of distribution = 6.0204.

and is superimposed on the histogram of the observed frequency distribution in Fig. 2. Frequencies graduated from this curve are given in Table 3, and calculation of the Chi squared function, after clubbing together frequencies of less than 7 at the tails of the curve, gives:

$$\chi^2 = 6.6183,$$

and entering Elderton's table at n' = 7 the value of the Pearson probability is:

$$P = 0.36$$

The modal value of σ_t at the minimum oxygen concentration in the Caribbean Sea region is calculated to be:

$$M_o = 27.171 \pm 0.007,$$

and since variations of three times the probable error are only rarely exceeded the limits of density (σ_t) level for the occurrence of the minimum oxygen value in the Caribbean Sea region is, tentatively:

$$\sigma_t = 27.150 \text{ to } 27.192,$$

which is very close to the value calculated for the western basin of the North Atlantic.

Application of the Trigometric Polyonomial to Time Series of Temperature Observations

Evidence of the nature of time variations of oceanographic elements (as temperature, salinity, etc.) at fixed depths (from the physical sea surface) in the North Atlantic, is brought out by analysis of results of a 24 hour series of continuous temperature observations at a position about 200 miles north west of Bermuda ("Atlantic" Station 2639: 35° 07'N, 66° 25'W). The variations were due chiefly to submarine waves of three different frequencies having periods of 24, 12, and 8 lunar hours, the amplitudes and phase angles being determined from the empirical data by numerical evaluation of the coefficients of a finite number of terms of a Fourier Series by the method of least squares.

In the case under consideration the function, f(X), is graphically described by the curve fitted to the time series of observations and the representation obtained by fitting a finite number of terms:

$$f(X) = A_o + A_1 \text{ Cos } \frac{2\pi X}{T} + - - - - + A_k \text{ Cos } \frac{2k\pi X}{T}$$

$$+ b_1 \text{ Sin } \frac{2\pi X}{T} + - - - - + b_k \text{ Sin } \frac{2k\pi X}{T}$$

to a given set of equidistant points where the values of the coefficients A_o, A_1 - - - A_n, b_1, - - - bn_1, are determined by the method of least squares. This type of function is known as a trigonometric polynomial. It should be noted that values of the coefficients obtained in this manner may not be exactly the same as the resulting Fourier Series through the same points.

Thus, dividing the total range, T, on the X axis (say, 24 lunar hours) into n - 1 equal subdivisions, the value of each ordinate is obtained from the curve; that is, for the values

$$0, \ \frac{T}{n}, \ \frac{2T}{n}, \ - - - - \ \frac{(n-1)\pi T}{n}$$

of X, the corresponding values

$$Y_o,\ Y_1,\ Y_2,\ ---\ Y_{n-1}$$

of Y are obtained, and the number of points is greater than $2k + 1$. The equations which would be identically satisfied if the polynomial went through the n + 1 points are:

$$Y_o = A_o + A_1 + A_2 + -----+ A_k$$

$$Y_1 = A_o + A_1 \operatorname{Cos} \frac{2\pi}{T}\frac{T}{n} + A_2 \operatorname{Cos} \frac{4\pi}{T}\frac{T}{n} + --- A_k \operatorname{Cos} \frac{2k\pi}{T}\frac{T}{n}$$

$$+ b_1 \operatorname{Sin} \frac{2\pi}{T}\frac{T}{n} + ---\ -- + b_k \operatorname{Sin} \frac{2k\pi}{T}\frac{T}{n}$$

$$Y_{n-1} = A_o + A_1 \operatorname{Cos} \frac{(n-1)\ 2\pi}{T}\frac{T}{n} + ---+ A_k \operatorname{Cos} \frac{2k(n-1)\pi}{T}\frac{T}{n}$$

$$+ b_1 \operatorname{Sin} \frac{(n-1)\ 2\pi}{T}\frac{T}{n} + ---+ b_k \operatorname{Sin} \frac{2k(n-1)\pi}{T}\frac{T}{n}$$

In general, however, these equations cannot all be satisfied, there being n + 1 points and only 2k + 1 constants, but denoting the difference between the right and left hand sides of each equation by $M_o,\ M_1,\ --\ M_{n-1}$ then according to the theory of least squares the best fit will be obtained when:

$$M_o^2 + M_1^2 + M_2^2 + --- M_{n-1}^2 \quad \text{is a minimum}$$

Thus, since the only variable parameters are the constants,

$$A_o,\ A_1,\ ---\ A_k;\quad b_1,\ ---\ b_k$$

the partial deviations are calculated with respect to the $2k + 1$ constants in each equation and set equal to zero. This gives $2k + 1$ equations with $2K + 1$ constants, which may be simultaneously solved for the constants

$$A_o, \quad A_1, \quad A_2, - - - A_k; \quad b_1 \quad - - - b_k;$$

the final resulting equations are:

$$nA_o = Y_o + Y_1 + Y_2 + - - - - - + Y_n$$

$$\frac{n}{2} A_1 = Y_o + Y_1 \operatorname{Cos} \frac{2\pi}{n} + Y_2 \operatorname{Cos} \frac{4\pi}{n} + - - - + Y_{n-1} \operatorname{Cos} \frac{2(n-1)\pi}{n}$$

$$\frac{n}{2} A_k = Y_o + Y_1 \operatorname{Cos} \frac{2k\pi}{n} + Y_2 \operatorname{Cos} \frac{4k\pi}{n} + - - - + Y_{n-1} \operatorname{Cos} \frac{2k(n-1)\pi}{n}$$

$$\frac{n}{2} b_k = Y_1 \operatorname{Sin} \frac{2k\pi}{n} + Y_2 \operatorname{Sin} \frac{4k\pi}{n} + - - - + Y_{n-1} \operatorname{Sin} \frac{2k(n-1)\pi}{n}$$

As a final step the equations are put in the form:

$$C_o + C_1 \operatorname{Cos}(X - \alpha) + C_2 \operatorname{Cos}(2X - \alpha)$$

where the amplitudes, C, and phases, α, are connected with the A's and b's by the relations:

$$\alpha = \operatorname{Cot}^{-1} \frac{A}{b}$$

$$C = \sqrt{A^2 + b^2}$$

The equations characterizing submarine waves of three different frequencies, causing short period variations of oceanographic characteristics during the 24 hour period beginning 15^{h} 30' (L.C.T.) at three depths in the water column of Station 2639 are:

$$H_{20^\circ} = 55.4 + 7.4 \operatorname{Cos} \frac{2\pi}{24}(t-5.2^{h}) + 1.8 \operatorname{Cos} \frac{2\pi}{12}(t-5.8^{h}) + 5.6 \operatorname{Cos} \frac{2\pi}{8}(t-5.2^{h})$$

$$H_{17^\circ} = 430.4 + 27.5 \operatorname{Cos} \frac{2\pi}{24}(t-16.6^{h}) + 14.0 \operatorname{Cos} \frac{2\pi}{12}(t-5.2^{h}) + 9.4 \operatorname{Cos} \frac{2\pi}{8}(t-0.9^{h})$$

$$H_{10^\circ} = 802.4 + 24.7 \operatorname{Cos} \frac{2\pi}{24}(t-17.4^{h}) + 4.1 \operatorname{Cos} \frac{2\pi}{12}(t-10.4^{h}) + 2.3 \operatorname{Cos} \frac{2\pi}{8}(t-6.4^{h})$$

where, t, is the time in lunar hours after the lower culmination of the moon; amplitudes are given in meters.

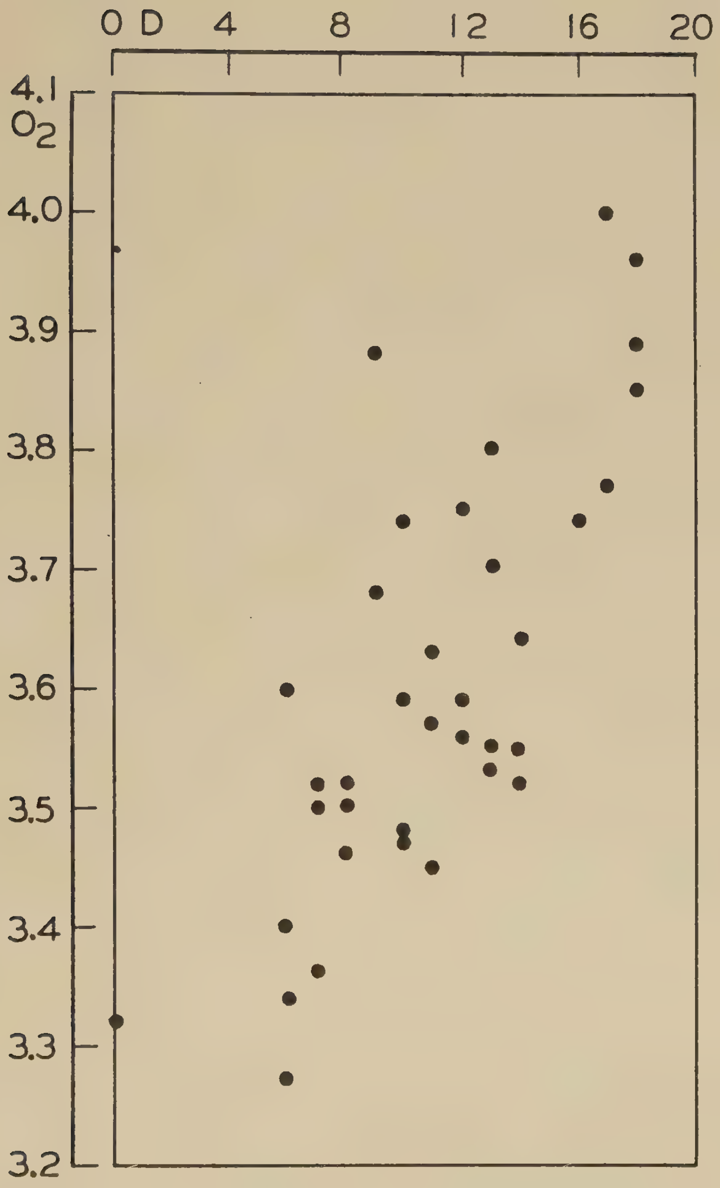


FIGURE 1. Correlation of D values and observed minimum oxygen values across the western North Atlantic basin between latitude 25° N. and 35° N. See text.

CLXXII

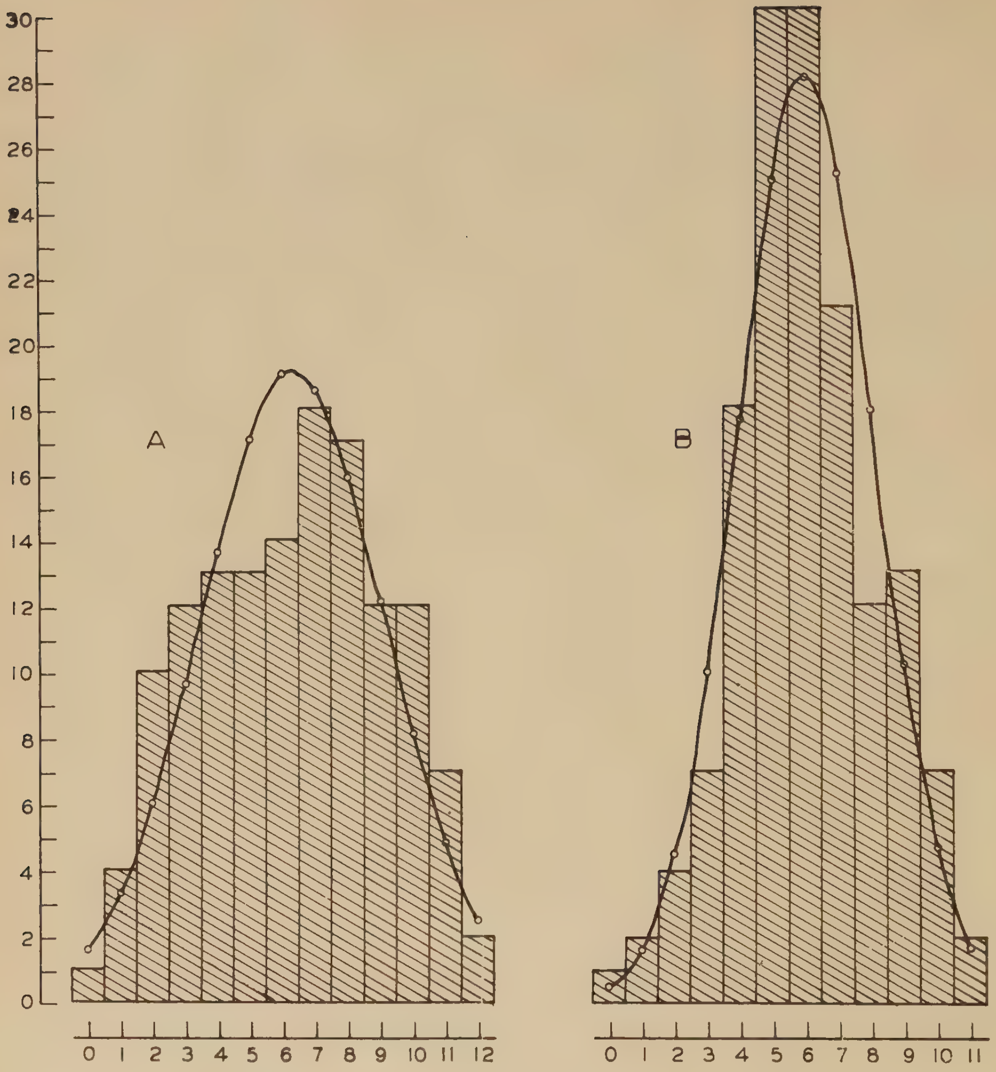


FIGURE 2. Frequency distributions of density (σ_t) values at observed depth of minimum oxygen concentrations; A = western North Atlantic basin, B = Caribbean Sea region. Observed frequencies given by histograms, theoretical frequencies by normal curves.

Contribution No. 218

RESULTADOS DE LA PRIMERA EXPEDICION EN LAS ANTILLAS DEL KETCH ATLANTIS BAJO LOS AUSPICIOS DE LAS UNIVERSIDADES DE HARVARD Y HABANA

Nuevo Género y Especies Nuevas de Foraminíferos

POR PEDRO J. BERMÚDEZ
Museo Poey, Universidad de la Habana.

En las siguientes líneas el autor propone un género y especies nuevas para la Ciencia de foraminíferos recientes.

Las ilustraciones que acompañan estos trabajos fueron hechas por mi estimado amigo el Profesor Sr. Alexander Bierig, a quien estoy muy agradecido.

Familia *Verneuilinidae*

Género **Barbourina** Bermúdez n. gen.

Genoholotipo, *Barbourina atlantica* Bermúdez n. sp.

Concha triangular en sección, con tres cámaras en las primeras vueltas y tres en las últimas; abertura anular en el centro de la cara terminal de la última cámara formando un tubo corto, protráctil y circular.

Tiene relaciones estrechas con el género *Bermudezina* Cushman,(1) del que difiere por ser triserial en todos los estados de su vida, mientras que *Bermudezina* tiene las últimas cámaras biseriales; la abertura en forma de tubo y circular es el carácter que relaciona más a estos dos géneros.

---

(1) Cushman, J. A., 1937, A Monograph of the Foraminiferal Family Verneuilinidae. Special Publ. No. 7, Cushman Lab. Foram. Res., p. 102.

Contribution No. 218 of the
Woods Hole Oceangraphic Institution

El género ha sido nombrado en honor del Dr. Thomas Barbour, Director del Museo de Zoología Comparada de la Universidad de Harvard, Cambridge, Mass. U. S. A.

Barbourina atlantica Bermúdez n. sp.

(LÁM. 1, FIGS. 1-4)

Concha alargada, fuerte, pared espesa, formada de granos gruesos de arena; triserial en sección transversal, aguzada en el extremo inicial y truncada en el extremo apertural que es el espacio más ancho de la concha; ángulos subagudos con tendencia a ser aquillados; cámaras numerosas, de dimensiones uniforme, aumentando de tamaño según se van agregando, bien diferenciadas, deprimidas, con suturas tan limbadas que sobresalen en alto relieve y visibles en número de seis parejas por cada cara lateral; abertura en el centro de la cara terminal de la última cámara, circular, protegida de un cuello corto y protráctil.

Largo 1.5 mm., ancho 0.7 mm.

Como se ha indicado arriba, este género nuevo está más relacionado con *Bermudezina* que con ningún otro conocido, por los caracteres que se describen en este trabajo.

La forma de la concha se asemeja más a *Gaudryina* (*Pseudogaudryina*) *jarvisi* Cushman(2) del Mioceno de Jamaica; a la que se parece por la forma y por el engrosamiento de las suturas de las cámaras, y se diferencia porque la especie de Jamaica tiene una porción de la concha triserial, y el resto biserial, mientras que nuestra forma nueva es toda triserial y la abertura es completamente distinta.

Tiene también algún parecido con *Bermudezina cubensis* (Palmer & Bermúdez),(3) del Oligoceno Inferior de Cuba; pero aquélla es más alargada, el estado triserial más pequeño, el biserial muy prominente y suturas simples.

El carácter de poseer suturas fuertemente limbadas se observa en muchas especies vivientes y fósiles de varios géneros de las familias *Verneuilinidae* y *Valvulinidae* en el área Caribe-antillana. Este carácter es muy acentuado en *Valvulina palmerae* Bermúdez.(4)

Localidad: Holotipo en Colección Cushman, Sharon, Mass. Atlantis Sta. 2960A, Bahía de Cochinos, Costa Sur de Cuba, 240 brazas de profundidad. (Lat. 22° 07′ N. Long. 81° 08′ 30″ W.) Febrero 18, 1938.

---

(2) Op. cit. p. 94, pl. figs. 6a-b.

(3) Op. cit. p. 103, pl. 14, figs. 9a-c.

(4) Bermúdez P. J., Mem. Soc. Cubana Hist. Nat. vol. 11, p. 139, lam. 16, figs. 1-3.

Paratipos en las colecciones del Museo de Zoología Comparada de la Universidad de Harvard, Cambridge, Mass., Museo Poey, Universidad de la Habana y en las colecciones privadas de Mrs. D. K. Palmer y del autor, Habana, Cuba.

Es frecuente en la localidad típica donde vive asociada a una rica y variada fauna de foraminíferos, sobre un fondo de restos de *Globigerinas*.

A continuación se da una lista de las estaciones donde ha sido encontrada, siempre más o menos frecuente:

ATLANTIS STAS.

2960A.	Lat. 22° 07′ 00″ N.	Long. 81° 08′ 30″ W.	240	brazas	de	profundidad.
2959.	Lat. 21° 17′ 00″ N.	Long. 83° 06′ 00″ W.	2050	„	„	„
2966.	Lat. 20° 47′ 05″ N.	Long. 80° 24′ 05″ W.	2125	„	„	„
2980B.	Lat. 22° 48′ 00″ N.	Long. 78° 48′ 00″ W.	225	„	„	„
2982.	Lat. 22° 48′ 00″ N.	Long. 78° 50′ 30″ W.	210	„	„	„
2983A.	Lat. 23° 11′ 00″ N.	Long. 79° 10′ 00″ W.	235	„	„	„
2995.	Lat. 23° 24′ 00″ N.	Long. 81° 00′ 30″ W.	605	„	„	„
2999.	Lat 23° 10′ 00″ N.	Long. 81° 29′ 00″ W.	230	„	„	„
3000.	Lat. 23° 10′ 00″ N.	Long. 81° 29′ 00″ W.	160	„	„	„

Familia *Chilostomellidae*

Género **Pullenia** Parker & Jones, 1862

Pullenia riveroi Bermúdez n. sp.

(LÁM. 2, FIGS. 1-6)

Concha subesférica; planispiral, algo comprimida lateralmente; compuesta de numerosas cámaras, que hacen varias circunvoluciones, con siete u otro cámaras, las que forman enteramente la última vuelta de espira, cámaras casi planas; suturas profundas con numerosos agujeritos, bien marcados y colocados en serie lineales en las suturas; superficie lisa y pulida, de color blanco lechoso; pared finamente perforada; abertura en forma de un arco semicircular, en la base de la cara septal de la última cámara, sobre el borde de las primeras cámaras de la concha, a menudo provista de una pestaña protectora en el frente de la abertura.

Largo 1.8 mm., ancho 0.75 mm.

Holotipo Colección Cushman, Sharon, Mass. Atlantis Sta. 2952 (Lat. 21° 52′ N. Long. 85° 00′ W.) 570 brazas de profundidad. Frecuente.

Además se ha encontrado frecuente en las siguientes estaciones:

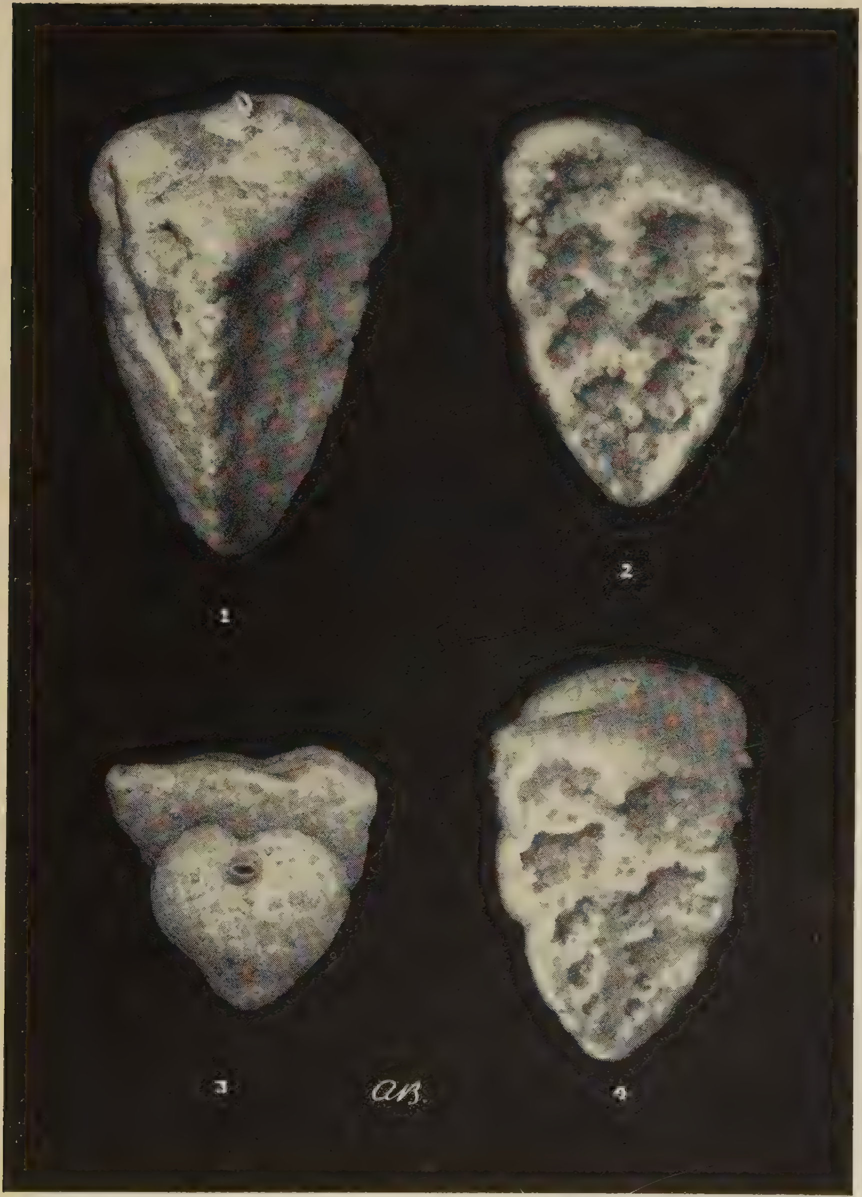
Atlantis Stas.
2971. Lat. 20° 34′ N. Long. 74° 24′ W. 810 brazas de profundidad.
2993. Lat. 23° 24′ N. Long. 80° 44′ W. 580 brazas de profundidad.

Los ejemplares jóvenes tienen la última cámara muy tenue y protuberante, tapando el área umbilical. Este gran desarrollo de la última cámara posiblemente es un flotador que utilizan en la primera edad para hacer vida pelágica. Cuando los ejemplares pequeños están desprovistos de esta cámara no se diferencian en nada de los adultos.

Las especies más próximas a la presente son: *Pullenia sphaeroides* (d'Orbigny) y *Pullenia quiqueloba* Reuss, que son muy conocidas por estar profusamente ilustradas por un considerable número de autores clásicos. Muy hermosas ilustraciones de estas especies se encontrarán en el Reporte del Challenger y en las monografías de Cushman.

Difiere de ambas especies en su forma más abultada, mayor número de cámaras, en poseer pequeños agujeros en las suturas de las cámaras y en presentar la forma juvenil una *cámara flotador* muy característica.

Me es grato nombrar esta interesante especie en honor del Dr. Luis Howell Rivero, Profesor de Zoología de la Universidad de la Habana.



Barbourina atlantica Bermúdez n. sp. × 40.

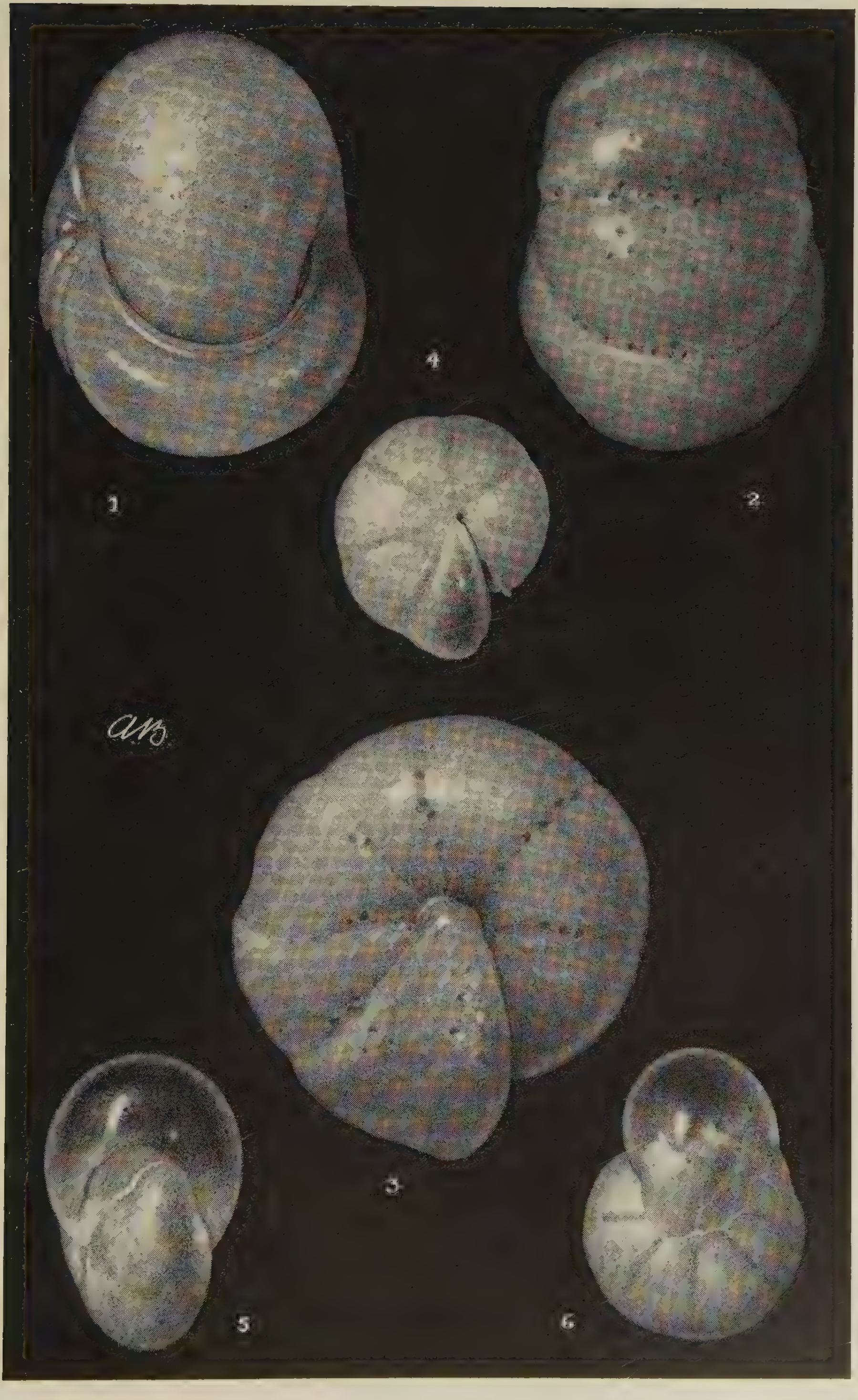
Atlantis Sta. 2960A (Lat. 22° 07′ N. Long. 81° 08′ 30″ W.)
Bahía de Cochinos, Costa Sur de Cuba, 240 brazas de profundidad.

Fig. 1, vista de canto; 2, vista de lado; 3, vista apertural; 4, Genoholotipo, vista de lado.

LAMINA 2

Atlantis Sta. 2952 (Lat. 21° 52′ N. Long. 85° 00′ W.)
570 brazas de profundidad.

Fig. 1, vista apertural; 2, vista dorsal; 3, Holotipo, vista lateral; 4, forma juvenil, vista lateral; 5, forma juvenil con la última cámara muy desarrollada, vista apertural; 6, forma juvenil, con la última cámara muy desarrollada, vista de lado.



Pullenia riveroi Bermúdez n. sp. × 31.

Contribution No. 219

Reprinted from the JOURNAL OF CELLULAR AND COMPARATIVE PHYSIOLOGY
Vol. 13, No. 3, June, 1939

THE DEVELOPMENT AND RESTORATION OF DEFICIENCIES IN THE PHOSPHORUS AND NITROGEN COMPOSITION OF UNICELLULAR PLANTS [1]

BOSTWICK H. KETCHUM
The Biological Laboratories, Harvard University, Cambridge, and the Woods Hole Oceanographic Institution, Massachusetts

There is little information concerning either the chemical composition of unicellular plants grown in deficient media or the recovery of the cells from the deficiencies acquired under such conditions, although the effects of the lack of essential elements on growth has been exten-

ula-
by
The
the
was
rp-
of
nic

Author's Correction

The development and restoration of deficiencies in the phosphorus and nitrogen composition of unicellular plants

Bostwick H. Ketchum

Journal of Cellular and Comparative Physiology, p. 380, vol. 13, no. 3, table 6, correct lines indicated—

for mg. P/gram dry wgt. read mg. P/10 mg. dry wgt.
for mg. N/gram dry wgt. read mg. N/10 mg. dry wgt.
for mg. C/gram dry wgt. read mg. C/10 mg. dry wgt.

ate
deficient in phosphorus can be produced by letting a culture grow in the light in a medium lacking phosphate. Cell division occurs under these conditions, though to a limited degree, and since no phosphate can be absorbed from the medium the cells thus formed are deficient in phosphorus. If phosphate is supplied the cells make up this deficiency. This occurs even in the dark, though the cells do not divide under this condition.

This deficiency may be called the phosphate or phosphorus debt. It may be measured by the amount of phosphate absorbed by deficient cells in the dark from a medium to which phosphate is added, or by direct analysis of the cells.

---

[1] Contribution no. 219 from the Woods Hole Oceanographic Institution.

MATERIAL AND METHODS

Stock cultures of the marine diatom, Nitzschia Closterium were prepared periodically in the medium described by Ketchum and Redfield ('38), and were grown in the light of a north window until used. An appropriate volume of one of these cultures was transferred to sterile sea water which had been enriched with the necessary quantity of phosphate for the purposes of the experiment. In general the experimental cultures were seeded with enough cells to give a concentration of 50,000 cells per cubic centimeter. Tests for bacteria were made by plating on the medium described by Reuszer ('33), as well as by the methods described by Barker ('35). All of the experiments reported were performed on bacteria-free cultures.

TABLE 1

The growth and phosphate absorption of a stock culture of Nitzschia Closterium in the light of a north window at room temperature (22° C.)

TIME *days*	CELL COUNT *cells/ltr*	PHOSPHATE CONCENTRATION *gamma/ltr*	DIVISION RATE (k) *days*$^{-1}$
0	5×10^7	4640	...
3.5	45.0×10^7	3380	0.63
4	64.0×10^7	2280	0.79
5.5	160×10^7	1075	0.57
6	209×10^7	(14)	0.54
7	275×10^7	0	0.27
8	377×10^7	0	0.31
12	400×10^7	0	0.01

The phosphate concentration in the medium was measured by the Deniges-Atkins ammonium molybdate method (Atkins, '23). Corrections for reagent blank and salt effect were always made (see Redfield, Smith and Ketchum, '37). The organic phosphorus in the cells was measured by the method described by Redfield et al. (l.c.).

EXPERIMENTAL RESULTS

Phosphorus deficient cells were obtained by growing a stock culture in the light of a north window after the cells had removed all phosphate from the medium. The growth of a typical stock culture and the coincident changes in the phosphate concentration in the medium are shown in table 1. The phosphate was absorbed by the growing cells, and decreased regularly until it was exhausted by the end of the fifth day. The growth of the cells, however, was not stopped by this complete exhaustion of phosphate. The division rate per cell is expressed by the velocity coefficient of the rate of growth (k) which is defined by the equation $k = 1/t \ln C_{t2}/C_{t1}$ in which C_{t2} and C_{t1} are the cell counts at the end and beginning of time t. After the sixth day the rate of growth decreased until the twelfth day when it practically ceased. Between the sixth and twelfth day, however, the cells almost doubled in number. Since no phosphate could have been absorbed during this time, the cells thus produced were deficient in phosphorus.

To determine whether such phosphorus deficient cells could absorb phosphate in the dark to satisfy their deficiency the following experiment was performed. Cells deficient in phosphorus were obtained from a culture which had been grown in the light of a north window for 11 days. They were suspended in fresh sea water enriched with nitrate and phosphate. The suspension thus obtained was divided in flasks, half of which were placed in the light of a north window, and half in the dark. Both sets of cultures were kept at room temperature. After various periods of time one flask from each of the two sets was removed and phosphate analyses and cell counts were made. The results are presented in table 2. Phosphate was absorbed rapidly by the cultures in the dark until the eleventh hour. After this time no significant absorption by the unilluminated cultures occurred. This absorption took place with no increase in the number of cells.

TABLE 2

Phosphate absorption by an 11-day-old culture under dark and light conditions at room temperature

Time	DARK			LIGHT			
	Count	Phosphate in medium	Phosphate absorbed	Count	Phosphate in medium	Phosphate absorbed	Extra abs. in light
hours	*cells/l.*	*gamma/l.*	*gamma/l.*	*cells/l.*	*gamma/l.*	*gamma/l.*	*gamma/l.*
0	41×10^6	179	0	41×10^6	179	0	0
2.5	41×10^6	137	42	44×10^6	126	53	11
3.5	40×10^6	126	53	45×10^6	108	71	18
5.0	42×10^6	109	70	49×10^6	80	99	29
11.0	40×10^6	73	106	70×10^6	33	146	40
18.5	44×10^6	71	108	85×10^6	26	153	45

Cell division occurred in the illuminated cultures and the absorption of phosphate in these was at all times significantly greater than in the cultures in the dark. Apparently the absorption by the illuminated cultures is composed of two parts; the absorption of phosphate necessary to overcome the deficiency and an absorption accompanying the growth due to the illumination. The former must have been the same in the light and in the dark, since the cells for both sets of cultures were obtained from the same suspension. The extra absorption in the light is coincident with the growth of the cells, that is with photosynthesis.

If the phosphate absorbed in the dark is that necessary to bring deficient cells back to their normal content of phosphorus, we would expect the amount so absorbed to increase with increasing age of the stock culture. Cells from cultures which had been grown in the light for various periods of time were transferred to fresh sea water enriched with phosphate. The phosphate concentration of each culture was measured when the cultures were made up, and after a period of 24 hours in the dark. The data presented in table 2 show that the absorption of phosphate in the dark is complete by this time. The results of this experiment are presented in table 3. The amount of phosphate absorbed in the dark per cell increases with the increasing age of the culture from which the cells were taken. This quantity is the amount of phosphate necessary for each cell to overcome its deficiency, and is called the phosphate or phosphorus debt.

TABLE 3

The amount of phosphate absorbed in the dark in a period of 24 hours by cells from stock cultures which had been grown in the light for various lengths of time

AGE OF CULTURE *days*	INITIAL PHOSPHATE *gamma/l.*	FINAL PHOSPHATE *gamma/l.*	PHOSPHATE ABSORBED *gamma/l.*	INITIAL COUNT *cells/l.*	PHOSPHATE DEBT *gamma/cell*
5	80	65	15	44×10^6	0.34×10^{-6}
5	80	59	21	60×10^6	0.35×10^{-6}
8	80	21	59	50×10^6	1.18×10^{-6}
11	179	73	106	41×10^6	2.56×10^{-6}
13	475	311	164	60×10^6	2.74×10^{-6}

The value of the phosphate debt agrees nicely with what one would expect from the data presented in table 1. The debt is very small on the fifth day, when there is still some phosphate in the medium in which the cells were grown. Between the fifth and eleventh days, when most of the growth in the medium devoid of phosphate occurs, the debt increases rapidly. Between the eleventh and thirteenth day, when little growth takes place, the debt increases more slowly.

The data so far presented indicate that the phosphate debt depends solely on the condition of the cells, and suggest that the quantity of phosphate absorbed in the dark is independent of the concentrations of phosphate in the medium. An experiment was performed to test this supposition. Cells from a 5-day-old culture were transferred to flasks containing fresh sea water enriched with phosphate. The condition and history of the cells were identical, the cultures differing only in the concentration of cells. These suspensions were placed in the dark at room temperature for 15 hours, and the phosphate absorption was measured as before. The data are presented in table 4. Although the cell concentration varied from 44 to 157 million cells per liter the amount of phosphate absorbed per cell was constant. The final concentration of phosphate varied between 28 in the culture with the most cells to 65 in the culture with the least. Obviously the amount of phosphate absorbed by the cells is independent of the phosphate concentration.

We may take the cell counts as a direct measure of the amount of cellular material present. Since the amount of phosphate absorbed is directly proportional to the number of cells present it appears clear that the phosphate absorbed is combining with some constituent of the cell. This material must be formed in photosynthesis, even when no phosphate is available.

TABLE 4

The amount of phosphate absorbed in the dark in a period of 15 hours by a 5-day-old culture in relation to the concentration of cells

INITIAL PHOSPHATE *gamma/l.*	FINAL PHOSPHATE *gamma/l.*	PHOSPHATE ABSORBED *gamma/l.*	COUNT *cells/l.*	PHOSPHATE ABSORBED/CELL *gamma/cell*
80	65	15	44×10^6	3.4×10^{-7}
80	59	21	60×10^6	3.5×10^{-7}
80	44	36	110×10^6	3.3×10^{-7}
80	38	42	115×10^6	3.6×10^{-7}
80	28	52	151×10^6	3.4×10^{-7}

The absorption of phosphate in the dark is a very rapid process, proceeding much faster than the normal absorption in the light (see Ketchum, '39). It is possible therefore that the absorption of phosphate in the light, by cultures that will absorb no phosphate in the dark, is merely a measure of the rate of formation of the material which combines with the phosphate. Since the rate of photosynthesis can be readily controlled by regulating the illumination, this question was studied as follows. Cells from a culture which had been grown in the light of a north window for 5 days were resuspended in fresh sea water enriched with phosphate. The cultures thus obtained were placed in the dark for 12 hours so that the absorption of phosphate in the dark would be complete. The culture was then divided in flasks and placed in the constant temperature air bath described by Ketchum ('39) at 16°C. One culture was in light sufficient to cause maximum growth of the cells, the light reaching the others was reduced by placing the flasks in light proof boxes covered by one, two and three layers of ground plate glass. The relative light intensity reaching the flasks was kindly measured for me by Dr. George L. Clarke. The data are given in table 5. The rate of growth increased with increasing light intensity, and the absorption of phosphate appears to follow the same relation. When the figures for the absorption are reduced to the phosphate absorbed per cell formed, the values obtained are constant for all light intensities. The constancy of this figure indicates that the absorption of phosphate during photosynthesis is dependent on the formation of a cellular constituent which combines with the phosphate.

Since the data presented give no idea of the relative magnitude of the deficiency, an experiment was performed to determine the phosphorus content of deficient cells and the content after a period of absorption in the dark. Cells were obtained from a very old culture which had been grown in the light of a north window for 30 days, and were resuspended in sterile sea water enriched with phosphate and nitrate. The cells were analyzed for the total organic phosphorus content when this sub-culture was made up and after a period of 48 hours in the dark. The cell concentration was 28 × 10^7 cells per liter, and no significant change occurred during the course of the experiment. The initial organic phosphate in the cells was 176 γ PO_4 per liter of culture or 0.63 × 10^{-6} γ per cell. This had increased to 916 γ per liter or 3.27 × 10^{-6} γ per cell by the end of the 48-hour period. The phosphate absorbed was 2.64 × 10^{-6} γ per cell, a debt comparable to that obtained in the 13-day-old culture (see table 3). These analyses show that cells can be produced which contain only 19.3% of the 'normal' phosphorus. In other words the debt incurred may amount to as much as 80% of the total 'normal' phosphorus content of the cell.

TABLE 5

Absorption of phosphate by cultures of Nitzschia Closterium at various light intensities. Grown under constant illumination for 9 hours at 16°C.

LIGHT INTENSITY	INITIAL PHOSPHATE	PHOSPHATE ABSORBED	INITIAL COUNT	FINAL COUNT	INCREASE	PHOSPHATE ABS./CELL FORMED
%	*gamma/l.*	*gamma/l.*	*cells/l.*	*cells/l.*	*cells/l.*	*gamma*
100	110	90	5 × 10^7	10.2 × 10^7	5.2 × 10^7	1.73 × 10^{-6}
70	110	83	5 × 10^7	9.7 × 10^7	4.7 × 10^7	1.76 × 10^{-6}
50	110	69	5 × 10^7	8.7 × 10^7	3.7 × 10^7	1.86 × 10^{-6}
35	110	61	5 × 10^7	8.8 × 10^7	3.8 × 10^7	1.60 × 10^{-6}

When Chlorella pyrenoidosa is grown in the light in a non-nutrient medium cells are formed which contain only one-third of the normal phosphorus and one-half of the normal nitrogen content.[2] Both nitrate and phosphate may be absorbed in the dark, as well as in the light to overcome these deficiencies. Since the analyses of the nitrogen and phosphorus in this experiment were done on the dried cells, this confirms, by an independent method, the findings reported in this paper.

---

[2] This experiment was done in collaboration with Dr. A. C. Redfield, and forms part of an investigation aided by a grant from the Carnegie Foundation. The author gratefully acknowledges the assistance of Dr. Lois Lillick and Miss Rena Josie.

A mass culture of 8 liters of Chlorella pyrenoidosa was grown by the method described by Ketchum and Redfield ('38) until it reached a cell concentration of 53×10^9 cells per liter. A sample of this was centrifuged off and dried. The chemical composition of this sample is typical of the 'normal' condition of the cells. The cells from 5 liters of this culture were centrifuged off, resuspended in sterile tap water containing no added nutrients, and grown in the illuminated culture jar. After increasing threefold under these conditions the cells ceased growing. This culture was then divided into seven equal portions. The cells from one were centrifuged off and dried for analysis. This sample was taken as characterizing the deficient cells. The remaining six portions were divided in pairs. The first pair was enriched with phosphate, the second with nitrate, and the third with both phosphate and nitrate. One of each of these pairs was placed in the light, the other in the dark. After 24 hours under these various conditions each culture was harvested and dried for analysis.

This experiment shows the results of growth in 1) an adequate nutrient medium, 2) a non-nutrient medium, in which deficient cells are formed, and 3) in a medium in which the deficiency incurred can be partially or completely overcome. The chemical composition of the cells under these three conditions are given in table 6.

The figures in the second column characterize the cells grown in the adequate medium. In the third column the chemical composition of the deficient cells is shown. The total amount of carbon in the culture increased threefold during the deficient growth although the percentage carbon content of the deficient cells is similar to the normal. Although a slight increase in the total amount of both phosphorus and nitrogen was observed, the deficient cells contained only 50.8% of their normal nitrogen and only 38.2% of their normal phosphorus content. Nielson and Hartelius ('37) have observed similar variations in the nitrogen content of yeast grown in deficient media.

All of the cultures in the dark decreased in dry weight and total carbon content as would be expected. The data clearly show that the deficiencies can be made up in the dark. The phosphorus increased from 38 to 65.6% of the normal content in the culture containing both nitrate and phosphate. The nitrogen content increased from 50.8 to 81% of the normal in the culture containing nitrate alone.

The recovery from the deficiencies is increased by illumination. All of the cultures in the light increased in dry weight and in total carbon content. The phosphorus increased to 76.4% of the normal content in the culture containing both phosphate and nitrate. The nitrate increased to 139.2% of the normal in the culture containing nitrate alone.

The greatest deficiencies were obtained in the recovery cultures grown in the light with only one element present. Thus the phosphorus content of the cells grown in the light in the medium enriched with nitrate was only 20.8% of the normal. The nitrogen content of the cells grown in the light with phosphate added to the medium was 34.6% of the normal. The development of the deficiency in the tap water was apparently stopped by a joint effect of the absence of both ions.

TABLE 6

The development of Chlorella pyrenoidosa deficient in phosphorus and nitrogen, and the recovery from this deficiency in the light and in the dark

	NORMAL CULTURE	DEFICIENT CULTURE	RECOVERY CULTURES					
			Dark + PO_4	Dark + NO_3	Dark + N + P	Light + PO_4	Light + NO_3	Light + P + N
Dry weight—mg./l.	43.6[1]	120	116	109	113	174	200	217
Phosphorus								
mg. P/gram dry wgt.	0.283	0.108	0.169	0.091	0.185	0.194	0.059	0.217
per cent of normal	100	38.2	59.7	32.2	65.5	68.6	20.8	76.4
mg. per liter	1.24	1.30	1.96	1.00	2.09	3.38	1.18	4.70
Nitrogen								
mg. N/gram dry wgt.	0.596	0.303	0.247	0.483	0.422	0.206	0.832	0.672
per cent of normal	100	50.8	41.4	81.0	70.9	34.6	139.2	112.5
mg. per liter	2.61	3.62	2.86	5.28	4.75	3.58	16.61	14.60
Carbon								
mg. C/gram dry wgt.	4.82	5.09	5.03	5.12	4.92	5.16	5.14	4.85
per cent of normal	100	105.8	104.5	106.4	102.1	107.2	106.9	100.9
mg. per liter	21.0	61.1	58.1	55.8	55.6	89.9	102.7	105.4

[1] Corrected by cell counts to the final dilution.

The results of this experiment show clearly that nitrogen and phosphorus deficient cells of Chlorella pyrenoidosa can be obtained. These cells can lose as much as 80% of their normal phosphorus, and 65% of their normal nitrogen content. The deficiencies thus incurred can be restored by the absorption of nitrate or phosphate either in the dark or in the light.

The author expresses his sincere thanks to Dr. A. C. Redfield for his generous assistance and advice.

SUMMARY

1. When cultures of the marine diatom, Nitzschia Closterium are grown in the light in a medium containing no phosphate, phosphorus deficient cells are formed. These cells absorb phosphate rapidly in the dark for about 10 hours, after which no further absorption in the dark occurs.

2. The amount of phosphate absorbed in the dark by phosphorus deficient cells depends on the length of time the cells have been grown in the light with no phosphate in the medium. This quantity is called the phosphate or phosphorus debt, and is a measure of the deficiency to which the cells have been subjected.

3. The phosphate absorbed in the dark by phosphorus deficient cells is directly proportional to the number of cells present and independent of the concentration of phosphate in the medium. It appears that the phosphate so absorbed is uniting with some cellular constituent. This material must be formed in photosynthesis even when no phosphate is available for absorption.

4. The absorption of phosphate by illuminated cultures is directly proportional to the number of cells formed, suggesting that this absorption is also effected by the combination of phosphate with some cellular constituent.

5. When Chlorella pyrenoidosa is grown in the light in a non-nutrient medium cells are formed which contain only one-third of the normal phosphorus and one-half of the normal nitrogen content. Both phosphate and nitrate may be absorbed in the dark as well as in the light to overcome these deficiencies.

LITERATURE CITED

Atkins, W. R. G. 1923 Phosphate content of fresh and salt waters in its relationship to the growth of algal plankton. J. Mar. Biol. Assn. N.S., vol. 13, pp. 119–150.

Barker, H. A. 1935 Photosynthesis in diatoms. Arch. f. mikrobiol., Bd. 6, S. 141–156.

Ketchum, B. H. 1939 The absorption of phosphate and nitrate by illuminated cultures of Nitzschia Closterium. Amer. J. Bot., vol. 26. (In press.)

Ketchum, B. H., and A. C. Redfield 1938 A method for maintaining a continuous supply of marine diatoms by culture. Biol. Bull., vol. 75, pp. 165–169.

Nielsen, Niels, and V. Hartelius 1937 Untersuchungen über die Stickstoffassimilation der Hefe. VIII. Untersuchungen über die Stickstoffabgabe der Hefe wahrend des Wachstums. Comp. Rend. Trav. du Lab. Carlsberg, Ser. Physiol., vol. 22, pp. 23–47.

Osterhout, W. J. V. 1936 The absorption of electrolytes in large plant cells. The Botanical Review, vol. 2, pp. 283–315.

Redfield, A. C., H. P. Smith and B. H. Ketchum 1937 The cycle of organic phosphorus in the Gulf of Maine. Biol. Bull., vol. 73, pp. 421–443.

Reuszer, H. W. 1933 Marine bacteria and their role in the cycle of life in the sea. III. The distribution of bacteria in the ocean waters and muds about Cape Cod. Biol. Bull., vol. 65, pp. 480–497.

Contribution No. 220

(Reprinted in U. S. A. from Transactions of 1939 of the American Geophysical Union)

THE INFLUENCE OF VERTICAL AND LATERAL TURBULENCE ON THE CHARACTERISTICS OF THE WATERS AT MID-DEPTHS

C. O'D. Iselin

(Contribution No. 220 of the Woods Hole Oceanographic Institution)

In a previous paper (Iselin 1936) the writer considered that the temperature and salinity of the main thermocline layer (400-1200 meters) in the Sargasso Sea were mainly determined by vertical turbulence. At that time special significance was attached to the very consistent temperature-salinity correlation at mid-latitude stations from the western North Atlantic. Thus, when plotted on a temperature-salinity diagram, the great majority of the modern observations fell along a narrow and slightly curving path connecting the characteristics of the superficial layer with those of deep water. The fact that in the main thermocline the temperature-salinity correlation was somewhat fresher than a pure mixture of deep water and surface-water was thought to result from the inflow of relatively large volumes of subantarctic intermediate water which appeared to enter the Sargasso Sea in two ways. First, this low-salinity layer seemed to penetrate northward across the Northern Equatorial Current at mid-depths and second, a considerable volume of it was observed leaving the Florida Straits to be discharged into the Sargasso Sea along the southern edge of the Gulf Stream. In short, it was considered that the negative salinity-anomalies brought to the Sargasso Sea by the subantarctic intermediate layer more than counteracted the positive anomalies arriving at similar depths from the westward flow of water carrying Mediterranean characteristics.

While in this view the existence of lateral movements was recognized in the case of the subantarctic and Mediterranean layers, it was thought that only by the upward mixing of deep water could the apparently rapid renewal of the bottom-water be explained. Therefore, it seemed likely that through vertical turbulence everywhere in the Sargasso Sea deep-water characteristics were being transferred to mid-depths and blended with those of the superficial layers, a portion of this mixture being carried to the north in the northern branch of the North Atlantic Current. Only in this way did it seem possible to explain the high oxygen-content of the deep water, which seemed to demand a relatively rapid, large-scale vertical circulation.

Because of the very slight lateral gradients in the Sargasso Sea, it appeared doubtful in 1936 that lateral turbulence could possibly outweigh vertical turbulence in determining the characteristics of the waters at mid-depths. Therefore, the subantarctic and Mediterranean influences were thought of as mass-movements, rather than as the lateral transfer of these characteristics through turbulence. Since that time, a number of papers (Rossby 1936, Parr 1936 and 1938, Montgomery 1938) have been published emphasizing the rôle of lateral turbulence in the sea. Evidence has been brought forward (Rossby 1936, Sverdrup 1938) that the coefficient of lateral turbulence may be as much as a million times greater than that of vertical turbulence. The meteorological principle of isentropic analysis, which stresses lateral mixing on surfaces of constant density, assumes that lateral turbulence entirely surpasses vertical turbulence in determining the characteristics of the waters at mid-depths. The only serious objection to this point of view lies in the high oxygen-content of the bottom-water. Unless this water is mixed vertically and carried off to the north at a relatively rapid rate, it is difficult to understand how its rich oxygen-load can be maintained. Nevertheless, much evidence has accumulated in recent years that at mid-depths lateral turbulence is much more effective than was formerly supposed.

Montgomery's (1938) analysis of the observations of temperature, salinity, and oxygen from the region of the Northern Equatorial Current shows that at least down to the surface $\sigma_t = 27$ (400-700 meters) the principle of isentropic mixing is nicely confirmed. For the layers he studied, the characteristics of each surface of constant density could be traced upstream to where it

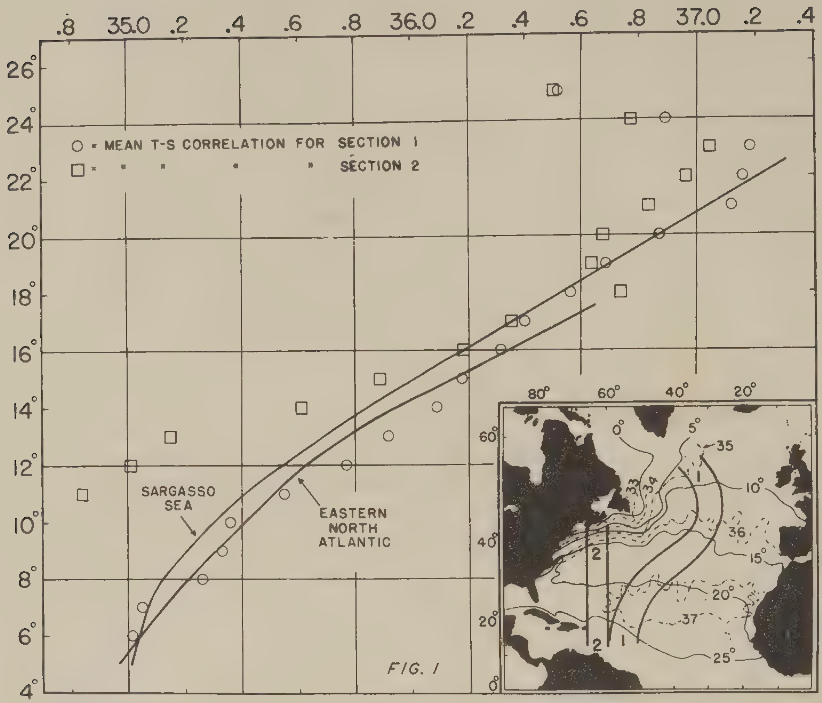


FIG. 1

cut the wind-stirred surface-layer. The question at once arises as to whether or not the same principle holds good for more northern waters and at greater depths. In other words, can the temperature-salinity correlation at mid-depths in the Sargasso Sea be explained by lateral turbulence, rather than by vertical turbulence accompanied by certain lateral mass-movements at mid-depths as described above?

The diagram presented here (Fig. 1) was constructed as a preliminary step in the study of this question. So many problems are involved that no single approach should be considered conclusive. Nevertheless, the outcome is on the whole favorable to the belief that lateral mixing has been sadly neglected until recently in most studies of the circulation-problem.

The temperature-salinity correlation of the sea-surface of course varies widely with the seasons. For the greater part of the North Atlantic and during most of the year a shallow secondary thermocline blocks off the surface-water from the deeper, main thermocline layer with which we are here concerned. However, at the underside of the shallow secondary thermocline the winter characteristics of the sea-surface persist almost unchanged throughout the year. It is not unreasonable then to suppose that the temperature-salinity correlation of the sea-surface in mid-winter has a special significance in determining the characteristics of the waters at mid-depths. This will be true whether vertical or lateral turbulence is the agency for the downward transfer of these characteristics.

Since the maximum cooling of the sea-surface is probably reached in March, a large chart was prepared on which both the March surface-isotherms and isohalines were plotted. These were copied from diagrams published by Böhnecke (1936). No doubt the temperature-chart is considerably more exact than the salinity-chart, for which much fewer observations were available. While the March surface-isotherms and isohalines in general parallel each other, the latter take a more wavy path so that there are many intersections. In addition, it is evident that in the western part of the ocean, especially north of the Gulf Stream System, the sea-surface in March is considerably fresher for a given temperature than it is in the east.

The temperature-salinity correlation along various north-south trending sections was next examined. Because of the wavy course of the isohalines, no single section seemed representative, but if the fresher waters north of the Gulf Stream are excluded, all temperature-salinity curves of the surface-layer in March more or less follow the mean vertical temperature-salinity curve (Iselin 1936) for the Sargasso Sea. In other words, the temperature-salinity correlation of the surface-layer of the North Atlantic in winter is not very different from the vertical temperature-salinity curve at stations in mid-latitudes. This fact, of course, has been generally appreciated for some time.

However, much closer and perhaps significant relationships are apparent, if the temperature-salinity correlation of the sea-surface in March is studied along a curving mid-ocean section that cuts the isotherms and isohalines at approximately right-angles. The path (inset chart in Fig. 1) of this section, which is about 300 miles wide, is also roughly at right-angles to the surface-currents. The mean temperature-salinity correlation along this band is indicated by the circles which are plotted on the diagram and it can be seen that for temperatures between 6° and 11° the points fall close to Helland-Hansen's (1926) curve for the eastern North Atlantic. On the other hand, for temperatures higher than 17° the surface-observations more closely follow the curve for the southern Sargasso Sea, the mean surface-salinity for intervening temperatures being considerably higher than either of the vertical curves. This would indicate that isopicnal mixing carries the surface-characteristics from the region northeast of the Grand Banks down to mid-depths in the area off the European Coast and that in the Sargasso Sea the upper layers are correspondingly influenced strongly by surface-conditions to the southeast.

It can be seen also from Figure 1 that, allowing for the uncertainty of the salinity-values (possibly as high as ±0.05 per mill, the temperature-salinity correlation of the surface-layer does not depart significantly from a straight line for temperatures between 6° and 23°. The Figure suggests that if the downward transfer of surface-characteristics by isopicnal mixing were the only process at work, the salinity of the main thermocline layer in mid-latitudes would be somewhat higher for a given temperature than is actually the case. Thus, if the lateral turbulence is the dominating mixing process, it is still necessary to call on the subantarctic intermediate layer to explain the relative freshness of the main thermocline in the Sargasso Sea. However, this need not be thought of as a mass-movement, for lateral mixing alone, if sufficiently vigorous, can transfer northward the fresher characteristics of the South Atlantic at mid-depths.

A further consideration of Figure 1 provides evidence that lateral turbulence only causes effective transfer of physical properties in a direction having a marked down-stream component. In other words, the relatively dense surface-waters of the southern Labrador Sea most closely resemble the temperature-salinity correlation at mid-depths off the European Coast, while the lighter surface-waters of the Northern Equatorial Current are found relatively unchanged at moderate depths in the southwestern Sargasso Sea.

The rather weak cross-current component of lateral mixing is further emphasized by a consideration of the temperature-salinity correlation at the surface along a north-south section, extending southward from the Nova Scotia Continental Shelf. The squares in Figure 1 show the mean temperature-salinity relationship in March along this band. North of the Gulf Stream in the so-called slope-water area the surface-waters have a density close to 26.5 in winter, but as it crosses the Gulf Stream this isopicnal descends to a depth of about 400 meters. It might be expected that lateral turbulence would carry the fresh, cold characteristics of the surface-layer north of the current downward and across it into the Sargasso Sea, just as it does in the case of the subarctic intermediate water further to the east. Only by assuming rather specialized conditions within the Gulf Stream west of the Grand Banks can this apparent paradox now be explained [Rossby (1936) has argued that because the Gulf Stream can be compared to a wake-stream and because the volume of the slope-water is rather small, the current will tend to absorb water along its southern side and to discharge water to the north. Thus, while the current is increasing rapidly in volume, the transfer southward of slope-water characteristics by lateral mixing may be blocked.]

The failure of lateral turbulence to transfer the very definite characteristics of the surface-layer of the slope-water band across the Gulf Stream is admittedly a puzzling point and one which seems unfavorable to a large coefficient of lateral mixing. A special study of this sector of the Gulf Stream is now nearly ready for publication, so the matter will not be enlarged upon here. However, except for the area between Cape Hatteras and the Grand Banks, the evidence presented in Figure 1 on the whole supports the newer conception of turbulence. It is apparently not necessary to depend largely on vertical mixing to explain the subsurface temperature-salinity correlation of mid-latitudes in the manner outlined at the outset of this discussion.

As explained above, the high oxygen-content of the deep water is a strong argument in support of vertical turbulence. No doubt both processes are working together and a great advance in our understanding of the circulation-problem will be made when the coefficients of vertical and lateral mixing can be approximately known for different degrees of stability and for currents of various strength. Until that day comes, it will probably be a mistake to favor either one or the other of these mixing processes.

As has already been indicated, provided the coefficient of lateral turbulence is assumed to be sufficiently large, it is not necessary to call on mass lateral movements at mid-depths to explain the observed salinity-anomalies. However, in this case it is necessary to assume a relatively deep current-system for the main anticyclonic eddy surrounding the Sargasso Sea. If the waters at depths near the layer of minimum oxygen are nearly motionless, there will exist only small frictional forces to cause the isopicnal mixing. Thus, before we can determine reliable mixing coefficients, we must settle the base-plane problem. It is hoped that in the near future this question can be brought to a more satisfactory state through a program of current-meter observations.

References

Günther Bohnecke, 1936, Temperatur, Salzgehalt und Dichte an der Oberfläche des Atlantischen Ozeans, Wiss. Ergeb. Deutschen Atlant. Exped. "Meteor", 1925-1927, v. 5, Atlas.

Bjorn Helland-Hansen and Fridtjof Nansen, 1926, The eastern North Atlantic, Geofysiske Publikasjoner, v. 4, No. 2.

C. O'D. Iselin, 1936, A study of the circulation of the western North Atlantic, Papers Phys. Oceanogr. Met., v. 4, No. 4.

R. B. Montgomery, 1938, Circulation in upper layers of southern North Atlantic deduced with use of isentropic analysis, Papers Phys. Oceanogr. Met., v. 6, No. 2.

A. E. Parr, 1936, On the probable relationship between vertical stability and lateral mixing processes, J. Conseil, v. 11, No. 3.

A. E. Parr, 1938, Isopycnic analysis of current flow by means of identifying properties, J. Marine Res., v. 1, No. 2.

C.-G. Rossby, 1936, Dynamics of steady ocean currents in the light of experimental fluid mechanics, Papers Phys. Oceanogr. Met., v. 5, No. 1.

H. U. Sverdrup, 1938, Research within physical oceanography and submarine geology at the Scripps Institution of Oceanography during April 1937 to April 1938, Trans., Amer. Geophys. Union, nineteenth annual meeting, 1938.

Woods Hole Oceanographic Institution,
Woods Hole, Massachusetts

Contribution No. 221

SOME PHYSICAL FACTORS WHICH MAY INFLUENCE THE PRODUCTIVITY OF NEW ENGLAND'S COASTAL WATERS

By

C. O'D. ISELIN

*Woods Hole Oceanographic Institution**

Of recent years physical oceanographers have gradually gained a more satisfactory understanding of the circulation problem. While it is true that most of this advance has resulted from studying the deep, oceanic currents, nevertheless, the newer principles also can be applied to the more difficult conditions found near the coast. More and more the physical investigators are working independently from the marine biologists. It is hoped that the following discussion of factors causing variations in the temperature and salinity of coastal waters off New England will demonstrate the biological significance of some of the modern physical investigations, and also perhaps help to bring the two branches of oceanography closer together again.

In general, coastal areas and oceanic areas differ fundamentally as far as the vertical distribution of salinity is concerned. Over the continental shelf the salinity usually increases with depth and, therefore, adds to the thermal stability of the water-column; while off shore in the deep water it decreases with depth and thus partly counteracts the stability resulting from the vertical temperature gradient. The fact that the salinity is at a maximum near the bottom on the continental shelf shows conclusively that the coastal circulation has an off shore component at the surface and an in shore component beneath.

The coastal waters, because of their relative freshness, are at most times of year less dense than the corresponding layer off shore and consequently a current is maintained which, for some reason not clearly understood, tends to have its greatest strength just outside the 100 fathom curve. This contour in general also corresponds roughly in position to the boundary between the two contrasting water-masses. The lateral transfer across the current, off shore at the surface and in shore along the bottom, supplies salt to the coastal waters which, because of land drainage, would otherwise gradually decrease in salinity. Off New England, coastal water can be defined as having a salinity of less than 34 °/₀₀, while higher values indicate an oceanic origin.

---

* Contribution No. 221.

Reprint from SEARS FOUND. JOURN. MAR. RES.

If the continental shelf were more regular in depth and width, and in the absence of fluctuations in the oceanic currents, the necessary interchange between coastal and off shore waters would probably proceed at a steady, slow rate and a continuous current would flow along the 100 fathom curve. However, uneven bottom topography and major barriers such as Nantucket Shoals and Cape Hatteras tend to prevent a continuous and steady southward movement along the edge of our continental shelf. In addition, a number of deep troughs allow saline, off shore waters to work inward along the bottom in certain areas almost to the shore line. A notable example occurs in the Gulf of Maine where only a few miles east of Cape Cod salinities as high as 34.2°/₀₀ are found at the bottom. In general, however, wherever the continental shelf is straight and regular, as off New Jersey, the cross current components are less pronounced and there is less possibility of sudden fluctuations in the in shore conditions.

The exchange of waters across the 100 fathom curve is partly brought about by small scale mixing processes which result in a rapidly changing temperature-salinity correlation across the boundary between the coastal and the oceanic waters. In addition, there are frictional movements having a much larger scale which from time to time cause considerable volumes of relatively fresh water to move off shore near the surface. These intermittent movements are of course accompanied by a corresponding bottom invasion of more saline water, although the compensation can occur at some quite distant part of the continental shelf. From the standpoint of a biologist, the irregularity and strength of these large scale mixing mechanisms are of great significance, for they are capable of causing the death of large numbers of the population living near the edge of the shelf.

There are at least two different causes for the sudden, large scale, off shore movements of coastal water. During the autumn and early winter, especially if the inflow from rivers is for some reason particularly weak, the density of the waters over the continental shelf may become identical with that of the corresponding layer beyond the 100 fathom curve. In this case the coastal currents will die away and the winds are then free to force large masses of the relatively fresh, but cold, water off shore. It is indeed surprising that our coastal waters do not blow off to sea much more often than they do. Apparently their very great stability prevents the winds during most of the year from breaking down the local gradient currents. As long as a current is maintained along the 100 fathom curve, the in shore waters are in some way confined. No doubt bottom friction also plays an important role.

A second and more effective mechanism seems to depend on the large, frictionally driven eddies that from time to time develop along the northern edge of the Gulf Stream. These powerful eddies are often as much as 60 or 80 miles in diameter and thus can extend the whole distance from the edge of the continental shelf to the Gulf Stream. They are known to occur north of the Gulf Stream at any point between Cape Hatteras and the Grand Banks, but they are most likely to be found off New York and off the Gulf of St. Lawrence. The structure of these eddies is as yet not well understood, nor is it known how long they persist. However, there is little doubt that, at least in their early stages, they can absorb large amounts of coastal water. This they mix with Gulf Stream water and thus produce a surface layer of intermediate salinity, typical of this zone between the current and the edge of the continental shelf. This band, in which only weak permanent currents are found, is known as the slope water. The intermittent eddies can extend to considerable depths, but it is in the surface layer that the contrasting tongues of coastal and Gulf Stream water are observed. Thus tropical plankton becomes mixed with forms from our coastal shelf and both drift off slowly to the northeast, parallel to the Gulf Stream. No doubt the intermediate temperatures and salinities are unfavorable to most of these animals and in any case, the larvae of commercial fish, which happen to be

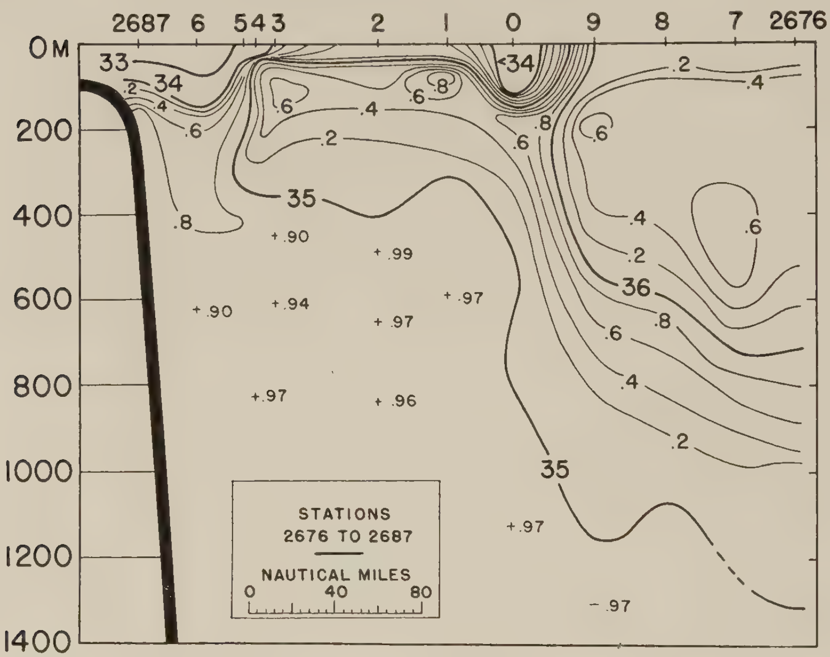


Figure 17. Salinity section, September 21–24, 1936, extending southeastward from the outer edge of Brown's Bank.

drawn into such eddies, will find themselves in deep water when the time comes to seek the bottom.

As yet no survey in the slope water area has had a sufficiently close station interval to reliably demonstrate the structure of these eddies. On several occasions, however, a single line of stations has crossed a body of almost undiluted coastal water as far off shore as the northern edge of the Gulf Stream (Figs. 17 and 18), but no direct observations are available to demonstrate whether such relatively fresh bodies of water are merely isolated pools or continuous tongues that have a connection with the waters over the continental shelf. In Fig. 17 almost pure coastal water can be seen at Station No. 2680 on the very edge of the Gulf Stream. This section was made in September 1936 on a line extending southeastward from Brown's Bank. Further to the eastward on the same cruise other bodies of coastal water were observed (Fig. 18) well beyond the continental slope. The positions of these stations, along with those of other sections made by the "Atlantis" within a two weeks period, are shown in Fig. 19. The latter diagram also demonstrates one possible interpretation of this survey. Admittedly the network of stations is so wide that any horizontal projection can be drawn in several different ways, but if any confidence is placed in the principles of isentropic analysis (Montgomery 1938), it seems likely that from Georges Banks eastward on this occasion there were several

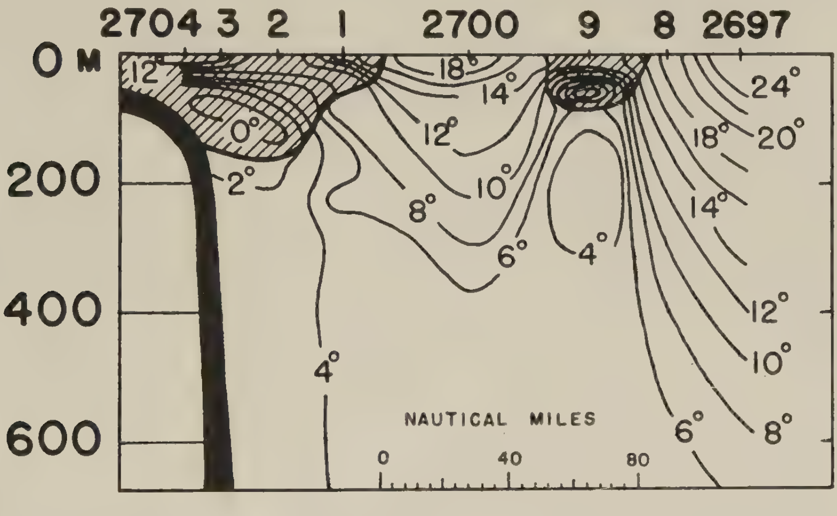


Figure 18. Temperature section, September 30–October 2, 1936, extending southwestward from the southern part of the Grand Banks. On this and subsequent sections the waters having salinities of less than 34°/oo are indicated by the cross-hatched areas.

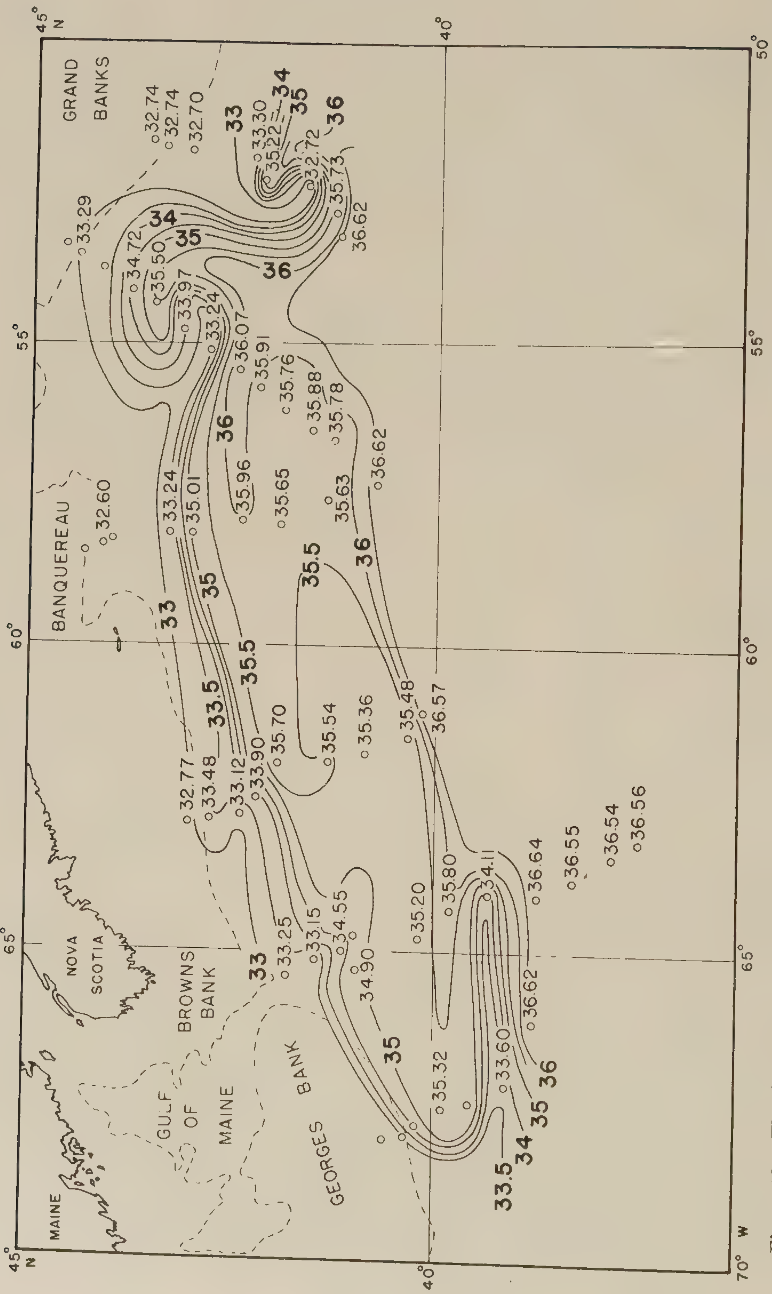

45° N
40°
50°
55°
60°
65°
70° W
GRAND BANKS
BANQUEREAU
NOVA SCOTIA
BROWNS BANK
GULF OF MAINE
GEORGES BANK
MAINE
33
33.5
34
35
35.5
36
32.74
32.74
32.70
33.30
35.22
32.72
35.73
36.62
33.29
34.72
35.50
33.97
33.24
36.07
35.91
35.76
35.88
35.78
36.62
33.24
35.01
35.96
35.65
35.63
32.60
32.77
33.48
33.12
33.90
35.70
35.54
35.36
35.48
36.57
34.11
36.64
36.55
36.54
36.56
35.20
35.80
33.25
33.15
34.55
34.90
36.62
33.60
35.32

Figure 19. The distribution of salinity on the surface $\sigma_t = 26$ in the eastern slope water area, September 15–October 11, 1936.

tongues of coastal water being drawn off into the eddies in the manner indicated.

While a satisfactory understanding of these large scale mixing processes must await more specialized observations, there is already ample evidence that from time to time (Walford 1936) and in various ways a considerable amount of bank water is carried off shore in the surface layer of the slope water band. Whatever the mechanism, such movements will be destructive to the plankton thus removed from the fishing grounds. In addition, it can be argued on theoretical grounds that such eddies will be more numerous during periods when the Gulf Stream is decreasing in strength. Thus there is some hope that the Gulf Stream studies now being made (Iselin 1938) may provide a basis by which the fisheries investigator can judge, or even foretell, the relative proportion of a given year class that will be lost in this way.

The long period fluctuations in the strength of the Gulf Stream, if indeed they do exist, will have a more direct effect on bottom temperatures and salinities both at moderate depths on the continental slope and on the deeper parts of the shelf. In both cases the exact characteristics of the bottom water depend largely on the depth of the main thermocline layer in the slope water band, and this in turn is dependent on the volume of the Gulf Stream. When the current increases in volume, bottom temperatures and salinites will fall; when it weakens, they will rise.

In the deep water north of the current, when undisturbed by an eddy, the main thermocline layer (12°–6°) usually occupies the depths between 100 and 500 meters. South of the Gulf Stream the same isotherms and isohalines are found at the 500–1200 meter level (Fig. 17). In the extreme and most improbable case that the current should die away completely, they would continue at approximately these deeper levels right in to the continental slope. A decrease of 50% in the volume of the current would cause the slope water thermocline to deepen to intermediate depths. That only a slight fluctuation in the depth of the main thermocline layer in the off shore waters will have a marked effect on bottom conditions along the continental slope at depths between 100 and 400 meters can be seen by examining Figs. 20 and 21. These show in cross section the coastal water, and the superficial layers of the slope water and the Gulf Stream. The stations were occupied in early June, 1937 and 1938, on a line extending from Montauk Point to Bermuda. While on these two occasions bottom temperatures differed by only about 4° at depths between 150 and 200 meters, it is evident that a more marked change in the off shore currents could cause even wider fluctuations. In addition, these sections illustrate two different stages in the development of eddies. In one case (Fig. 21) the swirl was swift and contains mixed water at its center. In the other case

(Fig. 20), the slope water currents were moderate, but almost undiluted coastal water had been carried well off shore.

No doubt the long period changes in strength of the Gulf Stream are so gradual that the bottom living population is easily able to migrate up and down the continental slope and thus remain in water of suitable temperature and salinity. But it is also possible that from time to time sudden fluctuations in the off shore currents can cause rapidly changing bottom conditions that might even result in the death of the less mobile forms. It can be argued that the famous destruction of the tilefish in 1882 along the outer edge of the continental shelf between Delaware Bay and Nantucket Shoals was due to this mechanism. In any case, there is a clear advantage for trawlers to obtain bottom temperatures when fishing in this critical zone.

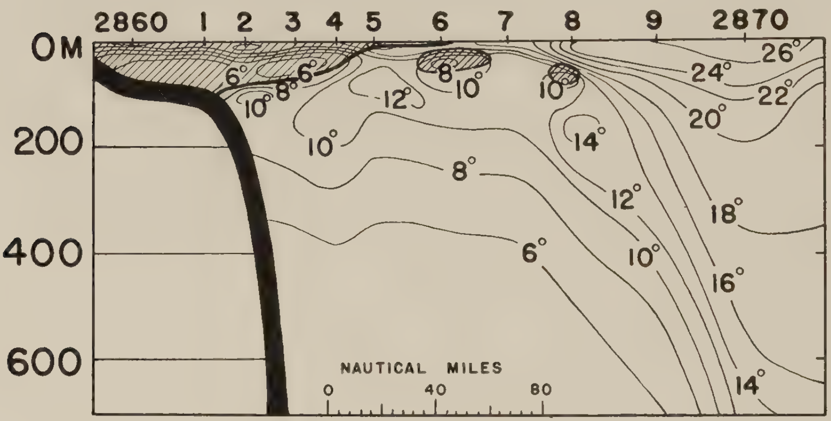


Figure 20. Temperature section, June 4–6, 1937, extending southeastward from Montauk Point, Long Island. Salinities less than 34°/oo are cross-hatched,

Although much of the bottom water on top of the shelf, especially throughout the spring and summer months, is directly supplied from the upper part of the off shore, main thermocline layer, the possibility of sudden changes in its characteristics is more remote. However, the in shore bottom population, because of the relative flatness of the shelf, has much less chance of adjusting its depth to meet the rise and fall of the off shore isotherms and isohalines which must accompany the fluctuations of the Gulf Stream.

The principles which we have discussed thus far only have an important effect on life in the superficial layers near the edge of the continental shelf and on bottom forms on the outer half of the shelf or a short distance down the slope. Are there any influences which can cause significant variations in the shallower waters nearer the coast? Obviously these must be much more under the control of the local climate and local mixing processes.

As mentioned already, throughout most of the year the waters over the continental shelf are extremely stable, both because of the off shore spread of relatively fresh water at the surface and because of the sharp, shallow thermocline layer which develops during the summer months. Under these conditions vertical turbulence is able to effect almost no transfer across the zone of maximum stability, just below the wind stirred, nearly homogeneous surface film. Thus as far as nutrients are concerned, the surface layer during the spring and summer cannot be supplied from beneath; and even at mid-depths the vertical transfer of essential chemicals must be extremely slow.

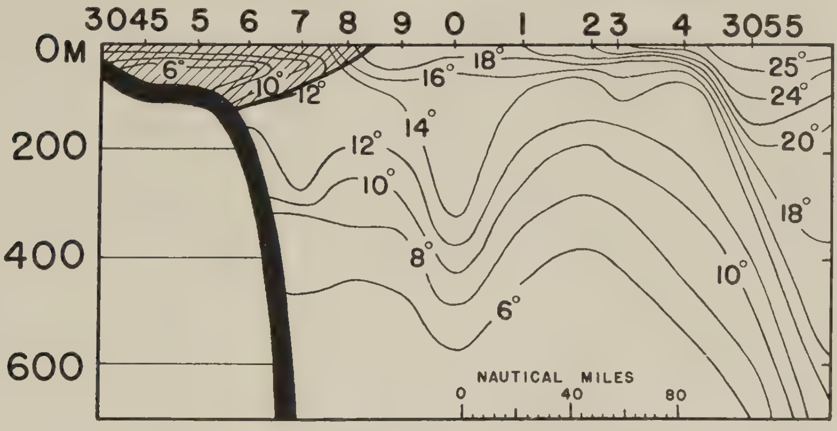


Figure 21. Temperature section, May 28–June 2, 1938, extending southeastward from Montauk Point, Long Island. Salinities less than 34°/oo are cross-hatched.

During the last few years physical oceanographers have begun to appreciate the important role which lateral turbulence plays in the sea (Rossby 1936, Parr 1938). Under the conditions of high stability often found in coastal waters, the isopicnal transport of nutrients should prove a most fruitful study. The vital biological role that lateral turbulence plays in the open ocean has been pointed out by Redfield (1936), and more recently (1939) he has studied this process from the point of view of certain planktonic forms in the Gulf of Maine. The chemicals which are in this way pumped up from mid-depths in the Sargasso Sea are transferred isopicnally across the Gulf Stream to the edge of the continental shelf. Thus as the bottom water penetrates landward, it carries with it a good supply of nutrients. But as long as the water-column is stable these cannot easily be transferred to the photic zone, because very few surfaces of constant density cut the surface of the in shore waters.

It has been pointed out by Parr (1936) that in layers where the stability is high, the lateral turbulence is increased. This principle should not be overlooked by planktonologists. It suggests that over the continental shelf the lateral spread of plankton will be particularly marked in the transition layer between the relatively light surface water and the heavier bottom water.

The resistance which the extreme stability of our coastal water offers to vertical turbulence was nicely illustrated by the recent New England hurricane of September 1938. Fig. 22 shows the temperature-depth curves from a station about 20 miles south of Montauk Point, Long Island, occupied on September 3 and again on September 29, 8 days after the gale. Although the center of the hurricane passed only a few miles west of this station, wind stirring was not able to break down the thermocline. However, turbulence did somewhat reduce the initial extreme temperature difference between surface and bottom.

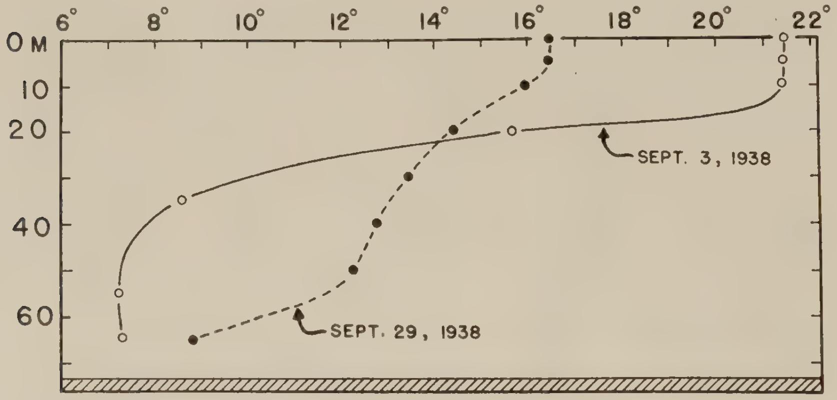


Figure 22. Temperature depth curves from a station about 20 miles southeast of Montauk Point, Long Island, before and after the New England hurricane of September 21, 1938.

The vital role which the breakdown of stability during the winter months plays in the fertility of the surface layer has often been emphasized, but it is less frequently mentioned that quite wide variations are possible from year to year in the effectiveness of the mid-winter stirring. Fig. 23 illustrates the cycle of temperature and salinity at a station in the western basin of the Gulf of Maine. At the surface the maximum cooling in this particular year (1934) came early in March. Although by mid-January the water was practically homogeneous down to 100 meters, a slight freshening

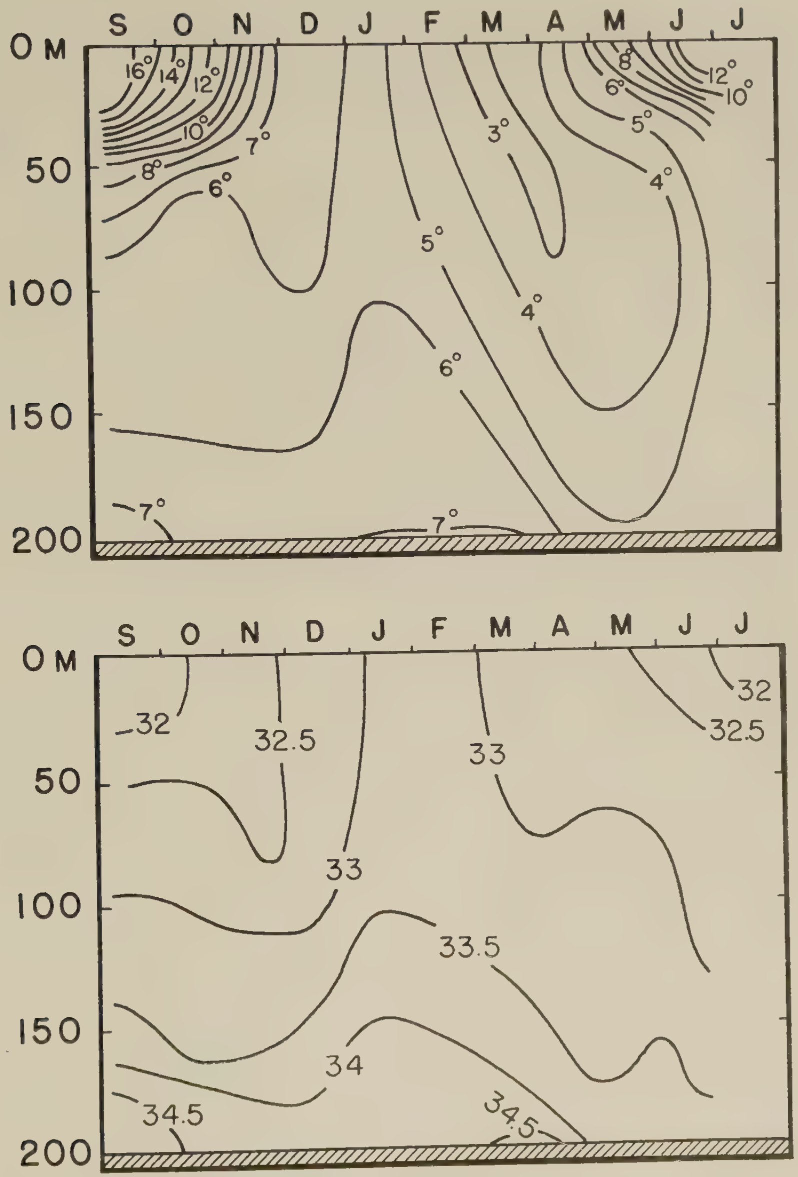


Figure 23. The changes in temperature and salinity, September 1933–July 1934, at a station in the western basin of the Gulf of Maine.

of the surface layer developed in February which retarded the downward transfer of minimum temperatures later in the winter. In addition, the temperature diagram shows that, because of the stability maintained by the vertical salinity gradient, turbulence did not bring minimum temperatures to depths below 100 meters until May. Meanwhile, the spring freshets and the early warming of the surface had begun to form a stable layer above. It is evident that the upward transfer of nutrients from the bottom would have been much more effective had the spring been delayed a few weeks.

That the winter overturn can be quite variable from year to year becomes clear when the factors which control vertical turbulence are considered. Obviously the colder the winter, the less stability will retard the deepening of the wind stirred surface layer. In addition, if the amount of river water spreading off shore at the surface is small, the stirring will also go deeper. Both factors tend to work together, for during severe winters much of the precipitation remains on the land in the form of snow and ice. In addition, during the short, critical period of minimum stability an especially heavy gale will do more to renew the fertility of the surface layer than all the winds of the other seasons. Finally, the longer the stability remains low, the better the chance of the mixing going to the bottom on the deeper parts of the continental shelf. These deeper gullies and basins contain a relatively rich supply of nutrients which will only be transported to the surface layer under conditions that are especially favorable to deep vertical mixing.

On the other hand, large areas of our continental shelf have a depth of less than 100 meters. In such regions the stability will completely break down early in the winter and there will be no chance of a supply of nutrients remaining on the bottom. In such cases the off shore spread of river water becomes the critical factor. If this occurs early and the winds are not strong enough to break through the fresher layer, then there is danger that before spring is well advanced the surface waters may become rather low in the essential chemicals. If such a winter is followed by an especially warm spring and summer, the plankton crop may be much below normal. The spectacularly poor mackerel season of 1937 was probably caused in this way. It has been pointed out (Settee 1937) that although on this occasion the stock of fish was sufficient, they were only caught during the summer months either very close to the shore, or on the outer banks. It seems likely (North American Council 1937) that only in these regions of strong tidal stirring could sufficient nutrients be maintained in the surface layer. Thus in order to secure food the mackerel were forced to change their usual migration route.

It is of course only natural that biological investigators should be interested in finding purely biological factors to explain the fluctuations in the fisheries. In such areas as Georges Banks, where, because of tidal stirring, the water-column remains homogeneous throughout the year, the annual variations in temperature, salinity and fertility are indeed very small. In fact, this is probably one of the main reasons for the tremendous fertility of Georges Banks. The chemicals are continually being returned to the surface layer. However, as has already been explained, because this bank is near the edge of the continent, it is in a vulnerable position from the standpoint of the slope water eddies. It remains to be seen whether or not this purely physical mechanism is sufficiently variable from year to year to explain a significant part of the variations in the catch.

REFERENCES

1. Iselin, C. O'D.
1938. Problems in the oceanography of the North Atlantic. Nature, Vol. 141, No. 3574.

2. Montgomery, R. B.
1938. Circulation in upper layers of southern North Atlantic deduced with use of isentropic analysis. Papers in Physical Oceanography and Meteorology, Vol. VI, No. 2.

3. North American Council on Fishery Investigations.
1937. Minutes of the Twenty-fourth Meeting, September 24–25, page 8.

4. Parr, A. E.
1936. On the probable relationship between vertical stability and lateral mixing processes. Journal du Conseil, Vol. XI, No. 3.

5. Parr, A. E.
1938. Isopycnic analysis of current flow by means of identifying properties. Journal of Marine Research, Vol. 1, No. 2.

6. Redfield, Alfred C.
1936. An ecological aspect of the Gulf Stream. Nature, Vol. 138, p. 1013.

7. Redfield, Alfred C.
1939. The history of a population of Limacina Retroversa during its drift across the Gulf of Maine. Biological Bulletin, Vol. LXXVI, No. 1.

8. Settee, O. E.
1937. Mackerel failure is due to scarceness of food. Fishing Gazette, Vol. 54, No. 12.

9. Walford, Lional A.
1938. Effects of currents on distribution and survival of the eggs and larvae of the haddock on Georges Banks. Bulletin of the U. S. Bureau of Fisheries, Vol. XLIX, No. 29.

Contribution No. 222

Reprinted from Biological Bulletin, Vol. LXXVII, No. 2, 285–296, Oct., 1939
Printed in U. S. A.

FURTHER EXPERIMENTS ON THE DECOMPOSITION AND REGENERATION OF NITROGENOUS ORGANIC MATTER IN SEA WATER[1]

THEODOR VON BRAND, NORRIS W. RAKESTRAW
AND CHARLES E. RENN

(*From the Woods Hole Oceanographic Institution, Woods Hole, Mass.*)

In an earlier paper we reported (1937) that the cycle of decomposition and regeneration of nitrogenous organic matter in sea water can be reproduced experimentally. The main stages in this cycle are: living organism—dead organism—ammonia—nitrite—nitrate—living organism. In view of the importance of nitrogenous material in the economy of the sea, it seemed worth while to carry these experiments somewhat further, and especially to consider the following questions:

1. Is it possible to reproduce more than one cycle in the same water?
2. Can the cycle be made shorter by eliminating certain stages?
3. Do successive cycles differ significantly in character or in rates of development?
4. In what ways do anaerobic and aerobic decomposition differ?
5. How completely can the changes observed in the different forms of nitrogen be accounted for in terms of each other; in other words, how constant is the quantitative balance?

Methods and Material

The plan of the experiments was the same as in our previous investigation. Organic material was suspended in sea water in large carboys and allowed to decompose in the dark, during which time chemical analyses were made periodically. Artificial cultures of *Nitzschia Closterium* were chosen as a source of organic matter, for our previous experience had shown these diatoms to be more satisfactory from an analytical standpoint than mixed plankton. Waksman, Stokes and Butler (1937) also used them successfully for a somewhat similar purpose. The diatoms were separated from the culture medium by centrifugation, washed several times with nitrate-free sea water, and finally suspended in a carboy of sea water which had been filtered through No. 4 sintered-glass. All experiments were carried out at the uncontrolled room temperature, varying from 15° C. in the winter to 25° in the summer. Before samples were removed for analysis the carboys were shaken vigorously to distribute the suspended matter evenly. When the latter showed any tendency to stick to the glass it was loosened with a rubber-tipped glass rod before shaking, after the rubber had been carefully cleaned to avoid contamination.

---

[1] Contribution No. 222 from the Woods Hole Oceanographic Institution.

The methods for the determination of particulate nitrogen, ammonia, nitrite and nitrate were the same as those used in our previous experiments and have already been described in detail.

The Possibility of Consecutive Cycles

In our previous investigation we found that the nitrate resulting from plankton decomposition could be regenerated into diatom protoplasm. This raised the question of the possibility of repeating such a cycle of decomposition and regeneration more than once in the same water. When the original plankton has undergone decomposition and the nitrate stage has been reached the water is inoculated with fresh *Nitzschia*. After about a week in the light an abundant growth is always observed. The nitrate drops to a minimum and when placed in the dark this newly-developed plankton undergoes decomposition again. In Series 12 three complete, successive cycles were carried out in this way. In another similar series, for which the data are not given, two cycles were completed, and in several others a part of the second cycle.

A poor diatom growth was observed after the second cycle in Series 12 (Table I), in which unidentified algae developed, among the *Nitzschia*.

It was important to know if a regeneration of phytoplankton material is possible in parts of the decomposition cycle other than the nitrate stage. During the plankton decomposition in Series 23, when the ammonia had reached its maximum, but before nitrite or nitrate had appeared, a portion of the water was transferred to another carboy (23A). After inoculation with *Nitzschia* and a week's exposure to light the ammonia had almost entirely disappeared and a heavy diatom growth had occurred. In a similar way Series 19A was removed from No. 19 before the nitrate had reached its maximum. Here, too, diatoms developed rapidly and abundantly and the soluble nitrogen compounds disappeared almost quantitatively. At these stages, at least, no toxic substances had been formed, or deficiencies developed, which could inhibit the development of phytoplankton. "Short-cuts" in the nitrogen cycle can evidently take place, and the possibility of their occurrence in nature suggests an explanation for

TABLE I

Series 12. Woods Hole harbor water. Fresh culture of *Nitzschia Closterium*. Quiet, in dark. Micrograms of nitrogen per liter.

Date	Particulate	Ammonia	Nitrite	Nitrate + Nitrite	Nitrate	Total nitrogen detd.	Diatom count × 10^3 per ml.
7–5–37	256	31	0	14	14	301	174
7	225	65	0	14	14		134
11	107	215	0				12
17	92		0	19	18		3
23	78		0	11	11		<1
30	49	260	0	11	11	320	<1
8–5	46		1	11	10		<1
13	45		5	25	19		<1
20	40	210	105	110	5	360	<1
24		70					
27	41	30	265	365	0	435	<1
9–2	31	13	350	355	5	402	
12			390	395	5		
25		25	370	390	20		
10–28	37	61	0	305	305	413	
31	Reinoculated with diatoms and put in light						
11–7							137
13							780
16	455	21	0	2	2	478	
16			Put in dark				
21							706
12–1	164						40
24		59	0				
2–1–38			1	8	7		
4		247					
24	189	246	1			(440±)	
5–6		0	70	350	280		
29			0				
6–25	142	12	1	300	300	455	
7–5	Reinoculated with diatoms and put in light						
12	408			80	80?	(490±)	
15				10			
18	489	0	0	40	40	529	
18			Put in dark			*	
29	304	115	0	25	25	445	
8–5	190	175	4	18	14	387	
12	202	110	45	50	5	362	
19	196	20	150	155	4	371	
25	208	10	170	160	0	388	
31	237	0	200	(160)	0	437	
9–13	260	18	0	300?	300?	578	

* Dissolved organic nitrogen = 370.

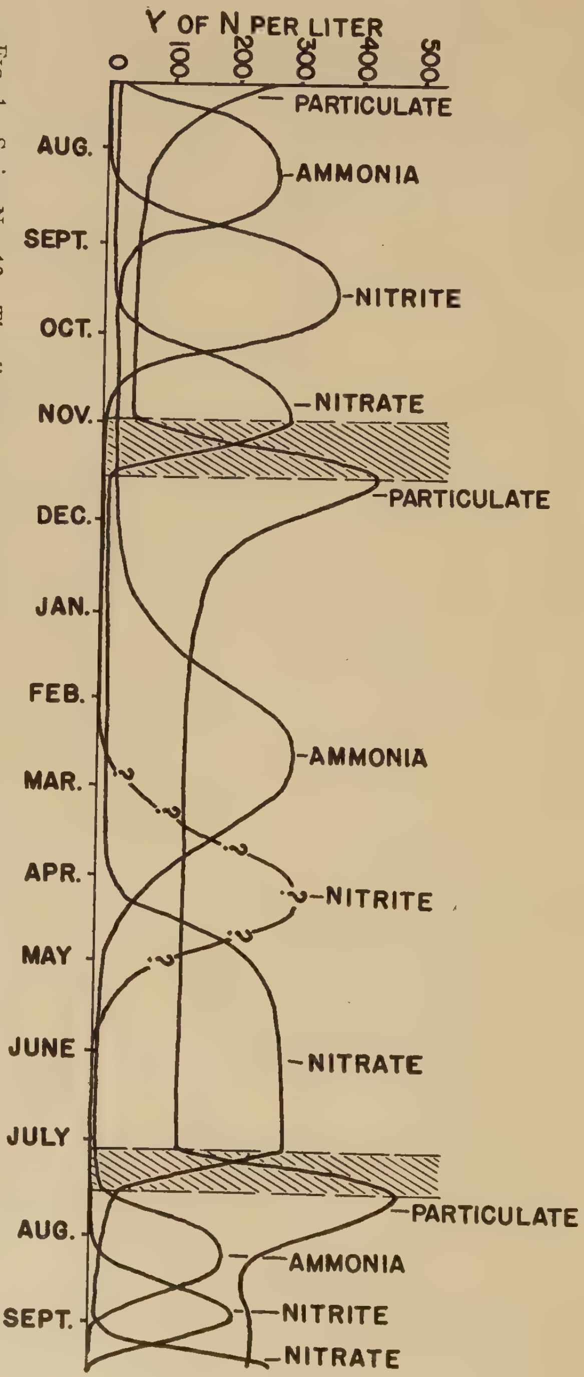


Fig. 1. Series No. 12. The disappearance of particulate nitrogen and the simultaneous changes in ammonia, nitrite and nitrate, plotted against time. Source of organic matter, fresh culture of *Nitzschia Closterium* suspended in sea water from Woods Hole harbor. The shaded areas represent regeneration periods, with the culture in the light; the remainder, decomposition in the dark.

the rapid succession of great numbers of phytoplankton organisms belonging to different species. In nature, all stages of the cycle must be taking place simultaneously, and the momentary picture is simply one of equilibrium.

Chemical Observations

Decomposition of Particulate Nitrogen

The particulate nitrogen is that contained not only in diatoms, but also in bacteria and miscellaneous debris. This material began to decompose rapidly in all cases, as soon as the water was placed in the dark. It never disappeared entirely, however, but reached an apparently constant level after periods varying from two to six weeks. This was true not only in the first decomposition cycle but also in the subsequent ones. This residual material is very resistant to further decomposition, and consequently the level of residual particulate nitrogen is higher after each successive decomposition cycle. In the first cycle of Series 12, for example, the residual particulate nitrogen was about 40 γ per liter, in the second cycle about 150 γ, and in the third 200 γ. These amounts are about 16 per cent, 33 per cent and 41 per cent of the particulate nitrogen present at the beginning of each respective cycle. It seems not unlikely that under natural conditions in the sea the plankton is incompletely decomposed, and a large part of the particulate nitrogen found by von Brand (1938) in the deeper levels may be contained in such resistant or slowly decomposing plankton and bacterial residues. The occurrence of bacteria and debris in this resistant fraction is indicated by the fact that the quantity of particulate nitrogen does not consistently follow the diatom count. While the sum of particulate and ammonia nitrogen is fairly constant during the first part of the decomposition cycle, the diatom count falls off much more rapidly than does the particulate nitrogen. Nevertheless, in nature this refractory residue cannot be entirely resistant to decomposition, otherwise the insoluble nitrogenous material, in the water or on the bottom, would increase without limit.

A curious irregularity was observed in Series 25, which was aerated by a constant stream of pure air. After about six weeks of normal decomposition, accompanied by the appearance, first of ammonia and then of nitrite, the particulate nitrogen rose abruptly to its initial value and the ammonia and nitrite disappeared entirely. A microscopic examination, carried out for us by Dr. Lois Lillick, showed the presence of an enormous number of bacteria and a few flagellates. The diatoms had disappeared completely. This phenomenon must be attributed to the development of a peculiar bacterial flora, since we did not observe it in any other series, including No. 24, which contained the same water and plankton as No. 25 but differed only in not being agitated with an air-stream during the decomposition.

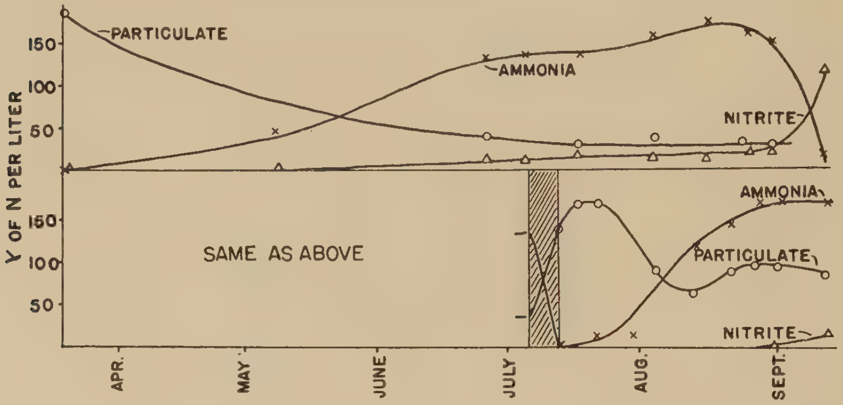
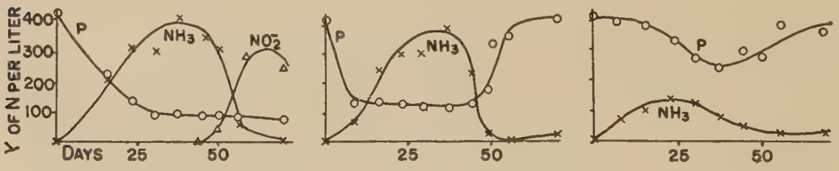


FIG. 2. Series No. 23 (above) and 23A (below). The disappearance of particulate nitrogen and the simultaneous changes in ammonia, nitrite and nitrate, plotted against time. Source of organic matter, fresh culture of *Nitzschia Closterium* suspended in sea water from the Sargasso Sea. The shaded area represents a regeneration period, with the culture in the light; the remainder, decomposition in the dark.



Series No. 24 Series No. 25 Series No. 26

FIG. 3

The disappearance of particulate nitrogen (*P*) and the simultaneous changes in ammonia and nitrite in cultures of *Nitzschia Closterium* in sea water from Woods Hole harbor. The three cultures were identical at the start. Series No. 24 stood quietly in the dark. Through No. 25 a continuous stream of purified air was bubbled. The air was completely removed from Series No. 26 and a continuous stream of purified hydrogen bubbled through it.

Ammonia

During the first decomposition cycle, in all cases, ammonia appeared in the water rapidly and in such amounts as to exclude the possibility of soluble nitrogen compounds intermediate between particulate nitrogen and ammonia. This but confirms our previous findings. But in the second cycle, although the particulate nitrogen disappeared at about the same rate, ammonia was not formed as rapidly as in the first. In Series 19A, for example, ammonia appeared only after 30 days of decomposition in the dark, during which time the particulate nitrogen had diminished by 160 γ per liter. The same behavior is found in Series 23A and in the second cycle of No. 19, and very likely also in the second cycle of Series 12, although the data are incomplete in the latter. These cases indicate the formation of soluble nitrogen compounds of higher molecular weight, intermediate between dead protoplasm and ammonia. Although there are two or three possible explanations for this lag in ammonia formation, we are not yet inclined to urge the acceptance of any one of them. It is also to be observed that the third cycle of Series 12 resembles the first in its more rapid rate of ammonia appearance.

In the first cycle it generally required from 16 to 25 days for the ammonia to reach its maximum, where it remained for a period of from 21 to 50 days before dropping. A notable exception, however, occurred in Series 22 and 23, in which the ammonia did not appear until about the forty-eighth day, required three to four months to reach its maximum, and remained for another two months before disappearing entirely. This unusually long duration of the ammonia stage would seem to be connected with the source of the water in the experiments. That used in Series 22 came from the Caribbean, and that in Series 23 from the Sargasso Sea, while in all other cases the water was taken from near the shore. Since the diatoms in all experiments were from persistent cultures the bacterial flora introduced with them was presumably constant, but whether the difference in decomposition is due to differences in the bacterial flora of the water itself or to such properties of the water as might influence the growth of bacteria, is not yet clear.

The lag in the oxidation of ammonia to nitrite in Series 22 and 23 was apparently not due to the absence of the necessary bacteria, for portions of these cultures were inoculated with 1 ml. from Series 12, in the midst of its nitrite stage, without any resulting change in the rate of nitrite formation.

Nitrite

In the first cycle nitrite began to appear in 31 to 58 days, corresponding to the beginning of the disappearance of ammonia. It reached its maximum when the ammonia had dropped to a minimum; that is, in a period of from 46 to 74 days. The total duration of the nitrite stage of the first cycle was quite irregular: two months from beginning to end in Series 12, but more than six months in Series 13 (See Table II). The lag in the latter case may in some way be related to the continuous aeration.

Our data concerning nitrite in the second cycle are too scattered to tell whether or not the rate of nitrite formation is the same in the second cycle as in the first. In the third cycle of Series 12 nitrite, like ammonia, developed rapidly.

TABLE II

Series 13. Woods Hole harbor water. Fresh culture *Nitzschia Closterium* in dark, with ammonia-free air bubbling through. Micrograms of nitrogen per liter.

Date	Particulate	Ammonia	Nitrite	Nitrate + Nitrite	Nitrate	Total nitrogen detd.	Diatom count × 10^3 per ml.
7- 8-37	269	43	1	11	10		234
10	380	11	0	17	17	407	274
13		115	0				
14	280						74
19	109	240	0	11	11	360	2
24	86	300	0	11	11		<1
31	60	310	0	11	11	381	<1
8- 5	53		1	11	10		<1
13	29		0	11	11		<1
20	25	400?	0	9	9	434	<1
24		360					
27	23	330	3	10	7	365	<1
9- 2	34	350	30	35	5	419	
12			330	340	10		
25		15	330	350	20		
10-28	7	82	345	(310)	?		
11-18			321				
2- 1-38		20	272	(260)	?		
24	74	20	232				
5- 6			0	400?	400?		
6-25	120	25	1				
7-15	118	74	7	230	225	422	
7-18		Put in light, not reinoculated					
8- 2	97	20	4	200	200		<1
4	Reinoculated with diatoms						
10	389	9	0	10	10	408	*

* No diatoms present; unidentified algae.

Nitrate

Nitrate begins to appear only when nitrite disappears, and this never seems to happen as long as a significant amount of ammonia remains. Since one cannot rely upon a greater accuracy than 10 per cent in the analytical determination, any quantitative balance is uncertain when large amounts of nitrate are involved.

Table III

Series 19. Woods Hole harbor water, collected 2–25–38. Fresh culture *Nitzschia Closterium*. Standing quiet, in dark. Micrograms of nitrogen per liter.

Date	Particulate	Ammonia	Nitrite	Nitrate + Nitrite	Nitrate	Total nitrogen determined	Diatom count × 10³ per ml.
2–25–38	316						
26		12	0	10	10	338	275
5– 6		41	12	25	13		
6–25	71	50	87	285	200	406	
7– 6		5	12		(Series 19A separated)		
15	48	15	1	350	350	414	
7–18	Reinoculated with diatoms and put in light						
29				17			
8– 2	396	0	0	10	10	406	56
8– 2	Put in dark						
10	451	0	0	15	15	466	240*
16	262	10	0	20	20	292	220†
23	201	30	0	15	15	246	
30	304?	15	1	20	19	339	
9–13	193	70	0				
Series 19*A*. Portion separated from Series 19 on 7–6–38. Reinoculated with diatoms and put in light.							
7– 6		5	12				
12	382	12	0	15	15	409	475
12	Put in dark						
18		0	3	25	22		350
21	396	7	0	10	10	413	
29	252	5	0	15	15	272	5
8– 5	221	90	0	15	15	326	
12	141	175	0	10	10	326	
20	208	186	0	10	10	404	
25	187	250	0	15	15	452	
31	201	250	0	20	20	471	
9–13	171	250	0	10	10	430	

* Few *Nitzschia;* mostly *Skeletonema Costatum.*
† Both *Nitzschia* and *Skeletonema.*

ANAEROBIC DECOMPOSITION

In addition to the experiments already described, which were carried out under aerobic conditions, the anaerobic decomposition of diatoms was also studied in two series. The carboys containing the water and diatoms were first evacuated to remove all the air from the water and the container. Then a slow, continuous stream of purified hydrogen was bubbled through the water. After decomposition in the dark for some time a strong odor of hydrogen sulfide was observed. In both cases the particulate nitrogen diminished very slowly, but remained constant at a level very much higher than that in the aerobic decompositions. The diatom counts also remained high; in fact, when Series 26 was discontinued, after 10 weeks, living diatoms were still found, which grew when placed in fresh culture medium.

TABLE IV

Series 22. Water from the Caribbean Sea. (18°–35′ N; 79°–14′ W); one year old. Fresh culture *Nitzschia Closterium*. Quiet, in dark. Micrograms of nitrogen per liter.

Date	Particulate	Ammonia	Nitrite	Nitrate + Nitrite	Nitrate	Total nitrogen determined	Diatom count $\times 10^3$ per ml.
3–18–38	123	0	0			125*	213
5– 6		25	0	10	10		
6–25	41	113	12	10	0	166	
7– 6		115	12				
13	22						
15		118	12	25	13		
8– 3	30	150	11	12	1	191	
13		145	12		(Series 22B separated)		
23	23	150	16	20	4	193	
30	30	125	30	30	0	185	
9–13		20	90			(150±)	

Series 22*B*. Portion separated from Series 22 on 8–13–38 and inoculated with 1 ml. from Series 12. In dark.

Date	Particulate	Ammonia	Nitrite	Nitrate + Nitrite	Nitrate	Total nitrogen determined	Diatom count $\times 10^3$ per ml.
8–13		145	12				
20		205	22	25	3	160	
30		210	36	35	0	245	
9–13		220	50			(270±)	

* Dissolved organic nitrogen = 93.

Ammonia also increased in this series for the first three weeks, and then gradually disappeared. In the other series no appreciable amount of ammonia was formed; on the contrary, a small amount of that originally present disappeared. This ammonia was not recoverable from the effluent hydrogen, nor are we able as yet to account for the behavior of ammonia in either of these series. As might be expected, no nitrite was formed.

After about two months under anaerobic conditions a portion from one of the cultures was aerated and kept henceforth aerobically.

Two months later a large amount of ammonia had been formed, but no nitrite or nitrate had appeared by the time the experiment was stopped.

QUANTITATIVE BALANCE

In our previous investigation we pointed out that in nearly every case studied the total determined nitrogen in the system (that is, the sum of the particulate nitrogen, ammonia, nitrite and nitrate) increased continuously throughout the period. In the cases we are now reporting the quantitative balance is much more satisfactory. In Series 13, 22, 23, 24 and 25 the changes in total nitrogen are small and probably explainable in terms of accumulated errors. In Series 12, 19, 19A, 23A and one other, the increase observed is too large to be accounted for in this way, but is less, relatively, than the increase noted in our first experiments. Previously, we discussed three possible explanations for this increase in total nitrogen: systematic errors in the determination of particulate nitrogen, the participation of dissolved organic nitrogen in the decomposition, and nitrogen fixation. We were in no position to prefer any one of these explanations. The fact that a good nitrogen balance was observed in half of our later experiments, including one which extended over more than a year, seems definitely to eliminate the possibility of systematic errors. The difficulty of determining dissolved organic nitrogen with any accuracy makes it almost impossible to test the second hypothesis directly. (The one determination given in the data for Series 12 was made, with some difficulty, by the method of Krogh, 1934.) However, we sought to investigate this question indirectly, by trying to see whether ammonia appears, on standing, in water devoid of gross particulate matter, and if so, whether the process is related to the content of dissolved organic matter. Two filtered samples of water, one from Woods Hole harbor and one from the Sargasso Sea, were placed in the dark and the usual determinations made periodically. Previous work had shown that the harbor water had a higher organic nitrogen content than water from the open sea, but there was no difference in the behavior of the two kinds of water. A small increase in nitrogen, about 60 γ per liter, was observed in both. This could indeed be the result of the participation of dissolved organic nitrogen, but we are inclined to believe that it is due to an entirely different cause. All the stored carboys were tightly stoppered, but before the removal of samples they were vigorously shaken and opened. During this time the water comes into contact with a rather considerable quantity of air, from which it may take up ammonia. To test this possibility, clean filtered air was aspirated for 12 hours through a sample of sterilized Sargasso water. This resulted in an increase of 50 γ of ammonia-N and 20 γ of nitrate-N. Such a quantity of ammonia is not surprising, in view of the amount of decomposing organic matter in this laboratory and its vicinity. It seems quite possible, therefore, that at least a large part of the increase in total nitrogen observed in some of our experiments may be due to contamination from the air. Nevertheless, this is not conclusive, and we are still in no position to exclude the possibility of either nitrogen fixation or participation of dissolved organic nitrogen. Atmospheric contamination was ruled out in Series 13 and 25, through which purified air was aspirated, and in these cases, indeed, the total nitrogen did not increase. Still, no increase was observed in Series 22, 23 and 24, which were not aerated, but which stood side by side with carboys in which nitrogen accumulated. Further work is still being done in the effort to clear up these discrepancies.

SUMMARY

1. Several consecutive cycles of decomposition and regeneration were carried out in the same water.

2. It is confirmed that in the first cycle the main stages of decomposition are: dead body—ammonia—nitrite—nitrate. In the second cycle there is evidence of intermediate soluble substances between dead body and ammonia.

3. Under anaerobic conditions the initial states of decomposition take place more slowly than under aerobic conditions, and no nitrite or nitrate is developed.

4. Regeneration of nitrogen into phytoplankton protoplasm is possible not only in the nitrate stage but also in the ammonia stage and before the nitrate has reached its maximum.

5. The quantitative nitrogen balance was better than that reported in previous experiments, and possible reasons for the discrepancies still present are discussed.

BIBLIOGRAPHY

von Brand, T., N. W. Rakestraw, and C. E. Renn, 1937. The experimental decomposition and regeneration of nitrogenous organic matter in sea water. *Biol. Bull.*, 72: 165–175.

von Brand, Theodor, 1938. Quantitative determination of the nitrogen in the particulate matter of the sea. *Jour. du Conseil*, **13**: 187–197.

Krogh, August, and Ancel Keys, 1934. Methods for the determination of dissolved organic carbon and nitrogen in sea water. *Biol. Bull.*, **67**: 132–144.

Waksman, S. A., J. L. Stokes, and Margaret R. Butler, 1937. The relation of bacteria to diatoms in sea water. *Jour. Mar. Biol. Ass'n.*, **22**: 359–373.

Contribution No. 223

(*Reprinted in U. S. A. from Transactions of 1939 of the American Geophysical Union*)

ATLANTIS CRUISE TO THE TROPICAL NORTH ATLANTIC, JANUARY TO MARCH, 1939

H. R. Seiwell

(Contribution No. 223 from the Woods Hole Oceanographic Institution)

In the winter of 1939 (January 18 to March 17) a detailed investigation of the physical structure of the tropical Atlantic waters, east of the Caribbean Sea region (to the 53rd meridian) was undertaken by the Atlantis. The area (Fig. 1) investigated, while hitherto practically unexplored, had been known from previous scattered observations to have representative members of all the major water mass-movements of the Atlantic circulation. In the uppermost layers of this area, circulation is dominated by the North Equatorial Current, and, extending down to depths of approximately 1000 meters, striking latitudinal transitions of oceanographic characteristics (caused by mingling of water-masses of diverse properties and origins) occur. Waters from this area entering the adjacent Caribbean Sea Region, through the passages among the Lesser Antilles, play a prominent rôle in the circulation of its upper 800 to 1000 meters.

In execution of the observational program, considerations based on existing information permitted the establishment of a network of stations designed to bring out information both on specialized and general problems. It was decided to limit depth of observations to 2000 meters, a procedure which permitted (in the allotted time) both a closer horizontal spacing of stations and a smaller vertical sampling interval. In the chart shown in Figure 1, stations occupied along the five lines were approximately 50 nautical miles apart, and vertical sampling intervals of the water-column were, for the most part, 25 meters or less for every other station; while vertical sampling intervals for the remainder of the stations varied between 50 and 100 meters. In this manner detail was obtained, permitting representation of conditions with but little interpolation, such as has not heretofore been done in the ocean-basins.

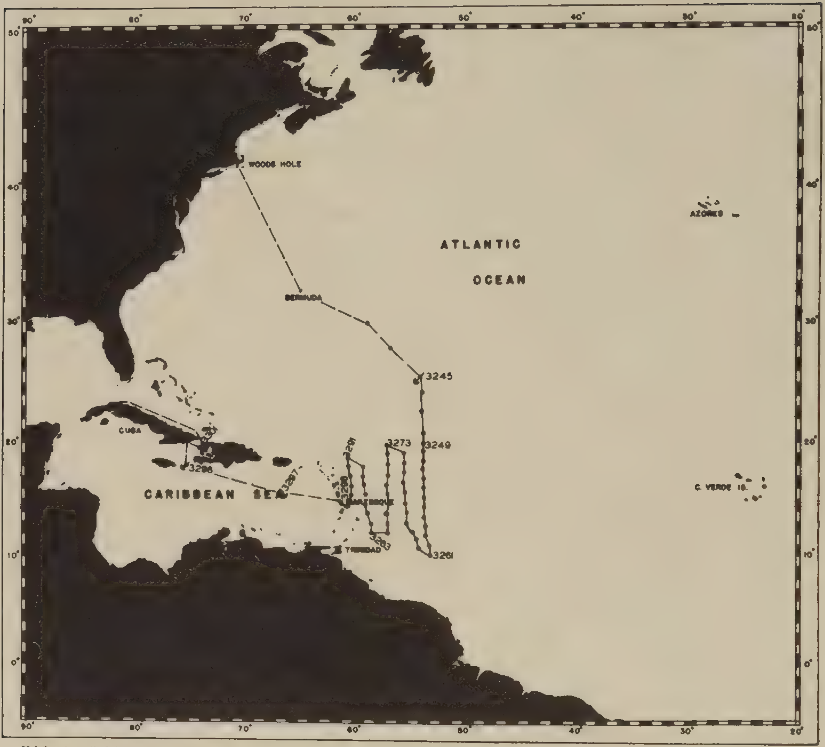


FIG. 1—ROUTE AND OCEANOGRAPHIC STATIONS OF "ATLANTIS" CRUISE TO TROPICAL NORTH ATLANTIC; BERMUDA TO HAVANA, CUBA, JANUARY TO MARCH, 1939

In presenting this brief resumé of preliminary results of the physical oceanography of this area, references concerning highly controversial subjects are dispensed with, and the procedure follows broad general outlines of generally accepted features of the Atlantic circulation. The discussion concerns only the properties of the upper 2000 meters (approximately 40 per cent of the mean depth of the area), but within this part of the water-column are found (in addition to the circulation-features of the upper layers) evidences of the presence of two of the five great water-masses which comprise a predominant part of the Atlantic circulation. The structural situation of the water-masses is illustrated by vertical distributions of salinity and oxygen (Stations 3246, 3250, and 3260) at the northern and southern extremities of the most easterly section (Fig. 2). Thus, at approximately 150 meters' depth the vertical salinity-distribution shows a well-developed maxima (diminishing in concentration from north to south), apparently representing the nucleus of water derived from surface-reservoirs of high salinity in the subtropics which later plays a prominent rôle in the Caribbean circulation.

Points of inflection, such as this, which mark maxima or minima concentrations in vertical distribution of oceanographic characteristics, may be used to analyze certain circulation-features of the ocean, and, in recent years, this type of analysis has been given prominence by the Berlin School of oceanographers in tracing water-movements over vast oceanic areas. However, when one is concerned with space-variations in concentration of maxima or minima in restricted and relatively small areas (such as the one under consideration) attention must be given to the fact that, for any observation on an inflection-point, the chances of obtaining the correct value of its concentration will primarily depend on the vertical gradients in its immediate vicinity as well as on the vertical sampling interval. Thus, in the case of the salinity-maxima in this area, the largest vertical salinity-gradients calculated in its immediate vicinity were 0.03 per mill to 0.04 per mill per meter, so that failure to sample the maximum point by, say, ten meters would cause a discrepancy ranging from 0.3 per mill to 0.4 per mill lower than its actual salinity-concentration. Thus, in drawing up the pattern of horizontal distribution of salinity-maxima in the area (Fig. 3), this consideration has been made and positions of the isohalines were primarily determined from observations of maximum salinity-concentrations where the sampling was most detailed; the dotted isohalines within the Caribbean Sea Region are based on Atlantis observations from 1937. A number of variations of this pattern may be obtained, but that shown in Figure 3 appears to be reasonable.

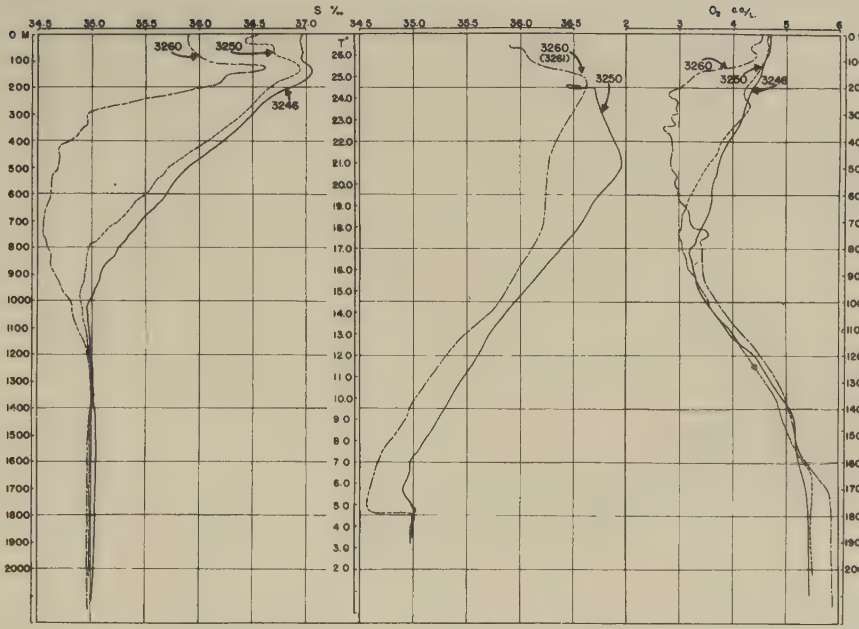


FIG. 2—VERTICAL DISTRIBUTIONS, SALINITY AND OXYGEN, "ATLANTIS" STATIONS 3246 (24° 24′ N, 53° 40′ W), 3250 (19° 16′ N, 53° 30′ W), AND 3260 (10° 58′ N, 52° 56′ W), AND TEMPERATURE-SALINITY RELATIONSHIPS FOR STATIONS 3250 AND 3260 [COMPOSITE CURVE ALSO BASED ON OBSERVATIONS FROM STATION 3261]

Current-arrows in Figure 3 indicate the general direction of drift (according to Montgomery's analysis [R. B. Montgomery, Papers Phys. Oceanogr. Met., v. 6, No. 2, 1938]), slight modifications having been made to conform to Atlantis records of navigation. The source of water-masses characterized by salinity-maxima, being chiefly in the subtropical surface-layer just northeast of the area investigated, may be considered as moving in an approximately west and southwest direction as the northern part of the North Equatorial Current. The concentration of salinity-maxima decreases along the route, by vertical and lateral mixing, and finally the water-mass enters the Caribbean Sea Region through the passages among the Lesser Antilles, chiefly north of latitude 15°. In the vicinity of latitude 15° and longitude 60° there would appear to be a recurving of this current, which is the source of the Equatorial counter-current. Such a recurving of the salt branch of the North Equatorial Current, just east of the Lesser Antilles, has been suggested previously, and the presence of a strong easterly surface-current in the southern part of the area is supported by Atlantis records of navigation. Between the salt northern branch of the Equatorial Current and the less-salt counter Equatorial Current, the low concentrations of maximum salinities near latitude 14° in longitude 53° (Station 3256) may indicate a westward intrusion of a "fresh tongue of the North Equatorial Current" carrying less salt water from the African coast.

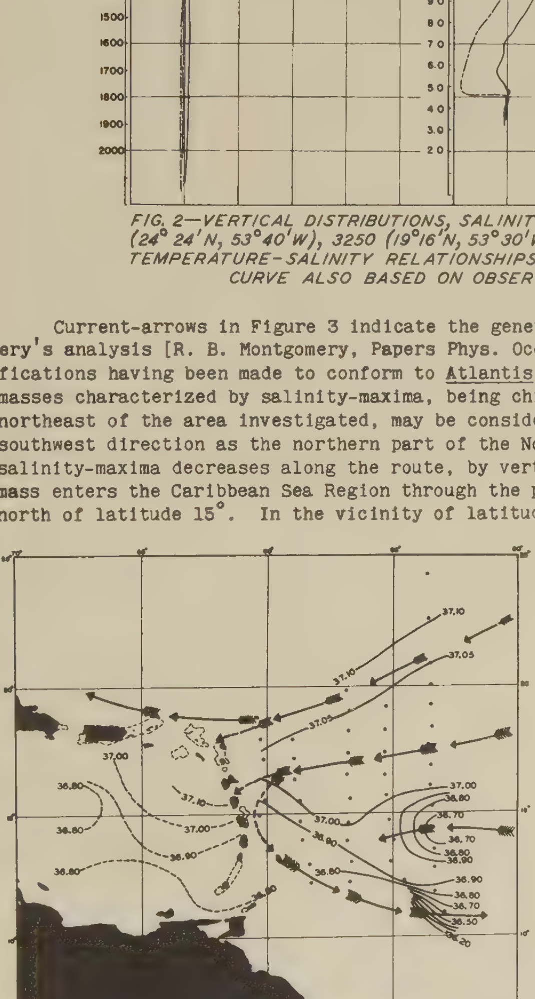


FIG. 3—PROBABLE SPACE-VARIATION IN CONCENTRATION PRINCIPAL SALINITY MAXIMA IN AREA OF INVESTIGATION [DASHED LINES WITHIN CARIBBEAN REGION BASED ON "ATLANTIS" OBSERVATIONS OF 1937]

This conception of the current-system in the upper levels of the area investigated is not in complete agreement with the conception of Defant [Albert Defant, Wiss. Ergeb. Deutschen Atlant. Exped. "Meteor" 1925-1927, v. 6, pt. I, 1936], who, in particular, places the origin of the Equatorial counter-current farther east (36° west to 44° west), outside the geographical limits of the area investigated, and who also does not consider the less saline

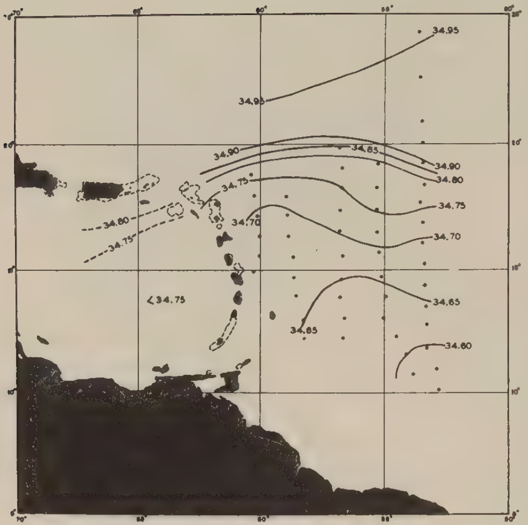


FIG. 4—PROBABLE SPACE-VARIATION IN CONCENTRATION OF MID-DEPTH MINIMA OF SALINITY

band of water north of the so-called counter-current as a part of the North Equatorial Current. The preliminary analysis of these new data in no way invalidates Defant's conception, although the records of navigation appear to throw some support toward the other view-point, particularly as regards the counter-current.

In the water at mid-depths, between approximately 750 and 1000 meters, vertical salinity-distribution (Fig. 2) shows a second point of inflection, marking an intermediate minimum of salinity-concentration, presumably representing relatively low-saline water of subantarctic origin, which has moved northward into the North Atlantic (subantarctic intermediate layer) [see Georg Wüst, Wiss. Ergeb. Deutschen Atlant. Exped. "Meteor" 1925-1927, v. 6, pt. I, 1935]. From south to north the concentration of this minimum point increases (Stations 3260 to 3246) and sinks deeper; at Station 3246 it has nearly disappeared, indicating that this latitude represents the northern limit of penetration of subantarctic water, although in the Caribbean Sea Region the mid-depth salinity-minimum is found everywhere and may be easily traced out through the Straits of Florida.

The pattern of space-variations of intermediate salinity-minima (Fig. 4) in the region investigated (mean depth = 813 meters) is more easily drawn up than that for the salinity-maxima, chiefly because smaller vertical salinity-gradients in its immediate vicinity allow more precise determinations of concentration. Outspreading of the water-masses so identified is towards the north and northwest. North of latitude 20° the subantarctic water is so diluted as to be scarcely recognizable (less than five per cent of the original water-mass is present); the main drift appears to be through the deeper passages among the Lesser Antilles, where it plays an important rôle in the Caribbean circulation. Within the Caribbean Region itself [H. R. Seiwell, Papers Phys. Oceanogr. Met., v. 6, No. 1, 1938], earlier observations have shown that, at the eastern end, the lowest intermediate salinity-value of 34.67 per mill increased along the route of the Caribbean Drift through the Caribbean and Cayman seas, the Yucatan Channel, and into the Straits of Florida (where the lowest minimum value encountered was 34.88 per mill).

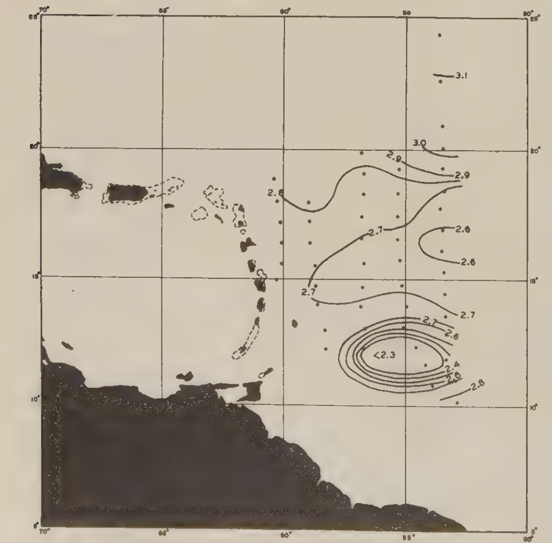


FIG. 5—PROBABLE SPACE-VARIATION IN CONCENTRATION OF PRINCIPAL MINIMA OF OXYGEN

Between the two water-masses, identified by maxima and minima of salinity, lies the principal minimum of oxygen-concentration at a mean depth of 516 meters (Fig. 2). Consideration of this characteristic is significant in physical oceanographical studies because of the ever present question: Does it or does it not identify a layer of practically motionless water? The former view adopted by certain of the Berlin School of oceanographers has led Defant [ibid.] to conclude that for the tropical Atlantic a motionless, or relatively slowly moving layer at mid-depths (characterized by the principal minimum of oxygen-concentration separates the oceanic troposphere (containing the principal salinity-maxima) from the deeper lying stratosphere (containing the intermediate salinity-minima). And, the adoption of this suggestion, when other possibilities exist [see H. R. Seiwell, Papers Phys. Oceanogr. Met., v. 5, No. 3, 1937], places definite restrictions on the derived circulation, particularly when use is made of geographical variations in dynamic topography to estimate horizontal current-patterns.

In the region investigated, curves for the vertical distribution of oxygen at northern and southern extremities of the most easterly section (Fig. 2) show significant latitudinal variations in oxygen-content; the minimum concentration of oxygen declines in value from north to south as its depth diminishes from approximately 800 to 350 meters. Thus, at mid-depths, the water in the southern part of the region has been far more depleted of its dissolved oxygen than has that occupying the northern part; at Station 3260 (at southern end of the area), for instance, there is but little difference in oxygen-content of the water-column between 200 and 600 meters, whereas at Station 3246 the minimum of oxygen is well marked out, and comparing vertical salinity- and oxygen-distributions at mid-depths, low oxygen-content in the south is seen to be associated with relatively low-saline water which has moved in from the region to the south.

The probable pattern of geographic distribution of minimum oxygen-values in the region investigated, as represented by Figure 5, shows the general north-south decline in concentration; two centers of low values occur, one represented by Stations 3253 and 3254 in the east central part and the other by Stations 3263, 3264, and 3282 in the southern part of the area. Thus, whatever water poorest in oxygen from mid-depths in the southeastern part of the area (associated with lower salinities) moves westward, toward the Caribbean basins, undergoes some rejuvenation by mixing with oxygen-richer (higher saline) water which has entered the area from the north.

Further examination of vertical salinity-distribution (Fig. 2) shows that everywhere in the area investigated, generally between depths of 1250 and 1350 meters, a third point of inflection marks out a secondary salinity-maximum. This characteristic, less prominent than the others, had a concentration-range (for the entire area) of only 34.99 per mill to 35.03 per mill, about 4 per cent of the intermediate salinity-minimum range. Its possible significance is that it apparently indicates the spreading out of the upper part of the North Atlantic Deep Current [see Wüst, ibid.] carrying relatively higher saline water southward to play a prominent rôle in the circulation of the Atlantic. The general direction of motion is approximately opposite to that of the layer identified by an intermediate salinity-minimum (it plays no obvious part in the circulation within the Caribbean Sea Region).

Diversity in character of water-masses entering into the circulation of the area investigated may further be brought out in sharp contrast by comparison of temperature-salinity relationships for two positions, 500 miles apart (Stations 3250 and 3260), along the most easterly section (Fig. 2). In the south, not only were salinities lower over the entire upper 2000 meters of the water-column, but, for any particular temperature, the associated salinity may be as much as 0.7 per mill less than that further north; and, this, coupled with extreme differences in content of dissolved oxygen, clearly shows that water-masses making up the circulation of this region are drawn from widely separated regions. As the water-masses of the upper 1000 meters or so move in a general westerly direction they combine so as to lose still more of their original identities so that within the Caribbean itself more uniform patterns are encountered.

In addition to the regular oceanographic observations, six stations were occupied for internal-wave observations (Fig. 1), five of which were made while the vessel was anchored (over depths of 5000 meters or more); each completed station consisted of 28 to 32 lowerings of 18 samples each, between surface and 1000 to 1100 meters, taken over approximately 25-hour periods. The average time between completed samplings of this water-column was 56.2 minutes. The sixth station (3299), worked while the vessel was drifting, was discontinued after 11 hours because of unfavorable weather.

In every case, large time-variations of oceanographic properties characterized observations at fixed depths (as measured from the sea-surface) and temperature-variations illustrate the magnitude of the phenomenon. During the five 25-hour observation-periods, maximum amounts of temperature-variations at standard depths ranged from 1°.19 to 2°.25 and the minimum variations from 0°.13 to 0°.31; the most frequent amount of temperature-variation at fixed depths during the 25-hour intervals was from 0°.6 to 0°.7. Thus, for instance, at Station 3245 (25° 32' north and 53° 45' west), the following ranges of temperatures were observed between 2^h 51^m, January 23, and 4^h 45^m, January 24, 1939 (GCT):

Depth	Temperature-range	Depth	Temperature-range
	°		°
0	0.60	600	0.63
100	1.31	700	0.63
150	2.35	800	0.66
200	0.32	900	0.32
300	0.36	1000	0.50
400	0.45	1100	0.24
500	0.57		

Previous evidence has indicated that variations of oceanographic characteristics (such as temperature) result from vertical displacements of the water-column, in which case temperature-variations at Station 3245 are related to vertical displacements (occurring during this time) of between 15 and 56 meters; whereas, at other stations in the series, vertical displacements of more than 75 meters are required to produce the observed time-temperature variations. Thus, since this phenomenon apparently occurs in all oceans, information of this kind is significant, not only for investigation of internal waves, but to assist in interpreting and estimating the significance of results of practical oceanographical investigations.

Woods Hole Oceanographic Institution,
Woods Hole, Massachusetts

Contribution No. 224

NOTES AND DESCRIPTIONS OF NEW DEEP-WATER MOLLUSCA OBTAINED BY THE HARVARD-HAVANA EXPEDITION OFF THE COAST OF CUBA. II(1)

BY W. J. CLENCH AND C. G. AGUAYO

This present report is a continuation of a previous paper(2) dealing, in the main, with mollusks collected by the *Atlantis* party in February and March, 1938, off the coast of Cuba. In this, as well as future papers, records and descriptions will be included of material obtained by the *Blake* and *Hassler* expeditions that have not been studied previously. A limited series of dredged material collected by the junior author and Dr. P. J. Bermudez at Gibara, Cuba, will be included.

During the winter of 1871-1872, the *Hassler,* under the leadership of Louis Agassiz, made a voyage from Boston to San Francisco by way of the Straits of Magellan. A few dredging stations were established in the West Indies in the vicinity of Barbados. Several stations were made off Rio de Janeiro, Brasil and south along the Argentina coast, mainly, however, in water under 100 fathoms. Very little of this material collected has ever been studied, though a few scattered records were included by Dall in his several publications on deep-water mollusca, but only a small portion of the total catch was seen by him. The remainder is still on hand, much of it unsorted.

The remaining *Blake* material is limited and only records that are additional to those in the reports of Dall will be included.

The large collections made by the *Atlantis* party, which contain several species that are new, indicate that the deep sea fauna of the West Indian region is anything but exhausted.

No really critical distribution patterns can be made, even of the common deep-water species, as so much of this vast area is still imperfectly or even wholly unknown. Practically every drag adds substantially to the distribution, bathymetric range and temperature data for any of several species, and the number of species runs into the hundreds.

---

(1) Contribution no. 224, Woods Hole Oceanographic Institution.

(2) Mem. Soc. Cubana Hist. Nat. 12, pp. 375-384, pl. 28, 1938.

However, such a large body of data has accumulated during the past several years on deep-sea mollusks of the world that it would be practically impossible for any one person to attempt to monograph the subject as a whole. Unlike the far more available inter-tidal species, the deep-sea forms are rare in collections and duplicate material is seldom exchanged. As a consequence, no museum collection contains more than a portion of the known species, and a surprising number of these still remain unfigured in the many scattered reports. These two factors alone indicate the difficulties encountered in such a study. For this reason, our attention will be almost wholly confined to the mollusk fauna of the Western Atlantic, and an attempt will be made in the future to bring together all of the information possible about several groups that occur within this area.

Solariella pourtalesi new species

(PLATE 28, FIG. 2)

Description: Shell rather thin, somewhat elongated, umbilicated and strongly sculptured. Color a dull white (all specimens collected dead) with a slight amount of opalescence indicated within the aperture. Whorls 6½, shouldered, regularly increasing in size and possessing a moderate pustulose peripheral keel. Spire extended, flat sided and forming a cone of 53°. Aperture subcircular, slightly angled at the termination of the peripheral keel and again at the mid area of the columella. The columella is thin, roundly arched and smoothly joining the base of the aperture. Lip simple and slightly flaring over the umbilical region. Umbilicus narrowly funicular and deep. Sculpture consisting of two spiral, pustulose carinae, one, the peripheral keel, and second, which is above, forms the margin of the whorl shoulder. A third and narrow thread-like carina exists below the peripheral keel but it is non-pustulose and forms the line along which the superior margin of the aperture is built. Nuclear whorl smooth and glass-like. Spiral striae very faint or wanting other than on the base of the body whorl. This is most strongly indicated near the aperture. Axial growth ridges fairly well developed, particularly on the base. Margin of umbilicus with two beaded or pustulose lirae, the inner one much the stronger. Upper slope of umbilicus with faint axial growth lines. Suture slightly indented, appearing to be deeply incised by nature of the pustulose shoulder.

Length	*Width*	*Aperture*	
7.8	6.1	2.8 × 2.5 mm.	Holotype
7.5	5.1	2.6 × 2.3 „	Paratype
7	5.3	2.6 × 2.5 „	„

Holotype: Mus. of Comp. Zoöl. no. 135,108, ''Atlantis'' station no. 2993 (N. Lat 23° 24′; W. Long. 80° 44′) off Cardenas, northern Cuba, 580 fathoms, March 15, 1938. Several paratypes from the same and the following stations:

''Atlantis'' Sta. 2999. N. Lat. 23° 10′; W. Long. 81° 29′, off Matanzas, Cuba. 230 fathoms.
''Blake'' Sta. 41, N. Lat. 23° 42′; W. Long. 88° 13′, off Bahía Honda, Cuba, 860 fathoms.
''Blake'' Sta. 46, N. Lat. 25° 43′; W. Long. 84° 47′, off S. W. Florida, 888 fathoms.
''Blake'' Sta. 2, off Morro Light, Havana, Cuba, 805 fathoms.
''Blake'' Sta. Yucatan Strait, 640 fathoms.

Dall had named the ''Blake'' material as *Solariella amabilis* Jeff., a species originally described from off the Shetland Islands, in 85-95 fathoms (25 mi. N.N.W. of Burra Firth Lighthouse, Unst). We are fortunate in possessing a series of cotypes of *S. amabilis* from Jeffreys and have found considerable differences existing between the two species. The error of assigning this name to the West Indian species was due to the figure of Jeffrey's which was apparently very much overdrawn. The artist attempted to indicate the very fine pustulation on the axial carinae (invisible to the naked eye) and consequently shows a strongly pustulose shell. *S. amabilis* possesses three carinae that are finely beaded as seen under a 14x lens. *S. pourtalesi* also possesses three carinae, the peripheral and superior alone being strongly pustulose or spinose, a character readily seen with the naked eye. The inferior carinae is smooth.

The proportions of both species are quite different. This is best noted on plate 28, figs. 1-2.

Calliostoma (Astele) hassler new species

(PLATE 28, FIG. 3)

Description: Shell solid and deeply umbilicated. Color a some what faintly mottled reddish brown. (The three specimens had been originally preserved in alcohol, and as a consequence, a change in color has probably taken place. Characteristic of the group, the color would possibly have been near a reddish tone.) Whorls 10, exceedingly regular in enlarging and having flat sides. Spire acute, extended, smooth in outline, forming a cone of 76°. Suture hardly discernible owing to the uniformity of the whorls. The whorls are really strongly carinated, though only apparent on the last whorl. Aperture subquadrate. Palatal lip simple, smoothly rounded at the outer base. Parietal wall very thinly glazed. Columella slightly arched above, thickened or narrowly folded, the fold terminating abruptly at the base. Umbilicus funicular, fairly wide and deep. Base of body whorl nearly flat at the parietal region, becoming more and more convex toward the end of the whorl at the aperture. Sculpture of numerous, fine, beaded, spiral threads (eight on the body whorl), between which are very fine and similarly beaded threads, the latter barely visible to the naked eye. Below the periphery of the body whorl (base of the shell) the beaded threads are all uniform in size, with the beads more closely set. The outer edge of the umbilicus is margined with a slightly wider thread. The umbilicus within is smooth.

Width	*Height*	*Aperture*	
31	30	14 × 14.5 mm.	Holotype
32	31.6	14 × 15 „	Paratype
25.7	25	9.8 × 11 „	„

Holotype: Mus. Comp. Zoöl no. 104,554, off Cabo Frio, Brasil (75 miles east of Rio de Janeiro) in 35 fathoms. *Hassler* voyage, January 20, 1872. A single paratype each in the Mus. Comp. Zoöl. and the Museo Poey, Habana, with the same data.

Remarks: This species is somewhat closely related to *Calliostoma jujubinum* Gmel. of the West Indies and Florida. It differs by being much larger with slightly finer sculpture and particularly in having a proportionately wider umbilicus. *C. hassler* is of a thinner and lighter structure and does not have the sutural (peripheral) ridges that generally characterize *C. jujubinum.*

Oocorys sulcata caribbaea new subspecies

(PLATE 29, FIG. 3)

Description: General characters similar to the typical form but differing by having a somewhat more extended spire and possessing a reticulated sculpture. The spiral ribs are coarser, more widely spaced and are crossed by axial threads that are very flat but thicken somewhat on crossing the spiral ribs. This produces a beaded, or lattice like surface. Nuclear whorls are smooth. Whorls 6 and globose.

Length	*Width*	*Aperture*		
41	29	21 × 12.5 mm.	Holotype	(M. C. Z.)
34 (+ 1 mm.)	25.5	18 × 10.5 „	Paratype	(M. C. Z.)
47	34	25 × 15 „	”	(M. C. Z.)
35.5 (+ 1 mm.)	26	18 × 11.5 „	”	(M. Poey)
31	22.7	15 × 8.5 „	”	(M. Poey)

Holotype: Mus Comp Zoöl. no 135,072, *Atlantis* station 2953, (N. Lat. 21° 47′ 30″; W. Long. 84° 32′ 30″) Bahía de Corrientes, Pinar del Río, Cuba, 615 fathoms. Feb. 10, 1938. Paratypes from this locality and from off Southeastern Oriente Province, Cuba (N. Lat. 19° 51′; W. Long. 74° 26′) 1600-1800 fathoms. March 5, 1938.

Remarks: The specimens that we have examined appear to differ quite definitely from *O. sulcata* Fischer as designated by Dall for the specimens obtained by the *Blake* off several of the Lesser Antilles. One specimen, from off Guadeloupe, collected by the Blake and named by Dall, is before us. The nuclear whorls in both *sulcata* and *caribbaea* are smooth and differ from the remaining whorls which are rather coarsely sculptured with numerous spiral ribs.

The present series of *O. sulcata caribbaea* are without any varices.

Dautzenberg and Fischer (1897, Mem. Soc. Zool. France 10, p. 162) have described a variety, *O. sulcata cancellata,* that is close to *caribbaea.* This variety differs, however, in having fewer and coarser axial cords than the typical form. It was described from off the Azores, occurring in 1600 meters. (Princesse-Alice, station 46).

Oocorys barbouri new species

(PLATE 29, FIG. 2)

Description: Shell solid, imperforate, somewhat extended and with a fine but strong spiral sculpture. Color a flat white with a broad band of dull brownish pink extending from the suture to below the periphery. Whorls 7 and rather strongly convex with a short and slightly concave shoulder. Spire extended, forming an angle of 55°. Aperture subovate, rather lengthened. Palatal lip broadly flaring or reflected. Parietal wall rather heavily glazed and forming a fold over the columella. The columella is moderately extended below to form a short canal and is slightly inwardly arched and slightly twisted. Suture but little indented, the whorls more or less shingled. Sculpture of numerous and rather fine spiral flattened costae crossed axially by exceedingly fine growth striae. The costa margining the shoulder is beaded, very much so on the earlier whorls. Nuclear whorls, however, entirely smooth.

Length	*Width*	*Aperture*	
50	29	34 × 16 mm.	Holotype
48.5	29	32 × 15 „	Paratype

Holotype: Mus. Comp. Zoöl. no 135,055, *Atlantis* station no. 2987, (N. Lat. 23° 22′; W. Long. 79° 53′) off Sagua la Grande, Cuba, 280-300 fathoms. March 13, 1938. Two additional paratypes have just been obtained during the 1939 expedition. These are from *Atlantis* stations, no. 3437 and no. 3451. The position of these two stations will be given in a later report.

Remarks: This species differs from *O. sulcata* and *caribbaea* by being more attenuated, having a bell-shaped lip and in possessing the broad band of color.

Latiaxis juliae new species

(PLATE 28, FIG. 4)

Description: Shell strong though not particularly solid, deeply umbilicated. Whorls 8, rather strongly convex. Color a flat white. Spire extended and acute, forming an angle of 55°, the last whorl free for nearly one-half its length (angle of whorl not including the elaborate sculpture). Aperture subcircular with a narrow, extended and slightly recurved canal. Lip simple with the parietal wall built forward, no true columella owing to the freedom of last whorl from the axis. Suture deeply incised from the 5th whorl onwards. Umbilicus circular and very deep, its outer and lower margins defined by a series of laminated flutings which are the lower and axial arranged thickenings of the spines. Sculpture of greatly produced recurved spines which project from the whorl periphory in an upward curve. These spines are hollow and are open for nearly their entire length on the aperture side. They are produced as folds which are not completely closed. A thickening of each spine continues on the whorl towards the base, ending as a series of laminated points which are somewhat flaring around the base of the umbilicus. Nuclear whorl probably smooth, but spines, as short points, develop immediately below and become greatly enlarged on the following whorls. Fine incised lirae are barely discernible under a 14 power lens.

Length	*Width*	*Aperture*	
28.2	16 (not including spines)	9 × 7.5 mm.	Holotype

Holotype: Mus. Comp Zoöl. no. 89,969, *Hassler* Voyage, off Sandy Bay, Barbados, West Indies, 75-100 fathoms. December, 1871.

Remarks: This species appears to be quite different from any heretofore recorded from the western Atlantic area. The lack of any appreciable spiral sculpture and the body whorl being free for ½ turn separates quite distinctly from the few species in this genus that occur in this region. A single specimen was obtained.

Tylotia cadenasi new species

(PLATE 29, FIG. 5)

Description: Shell solid, imperforate and attenuated. Color isabelline gray. Whorls 13 and moderately convex. Spire extended and acute. Aperture subauriculate with a rather lengthened canal below and a rather deep palatal notch at the superior margin. Parietal wall deeply glazed with a well formed tubercle above and at the base of the notch. Columella straight and heavy with a thickened area at the base on its outer side. Suture slightly indented. Sculpture of strong wing-like structures or alations, initiated first below the smooth nuclear whorls as broad and somewhat flattened axial ridges, which on the sixth whorl become slightly oblique and expanded and proportionately increase in length to the body whorl. Fine and somewhat wavy spiral threads are produced on the back of the alations, the inner face of each being smooth.

Length	*Width*		*Aperture*	
49	33	(including alations)	20 × 8 mm.	Holotype
52	30.8	„	21 × 7.6 „	Paratype

Holotype: Mus. Comp. Zoöl. no. 135,056 *Atlantis* station 2963, (N. Lat. 22° 07′; W. Long. 81° 08′), Bahía de Cochinos, Cuba. 180 fathoms. February 25, 1938. One paratype, from the same locality in the Museo Poey, and one from Atlantis station 2962-O, Bahía de Cochinos.

Remarks: This species is without question, very closely related to *T. johnsoni* Bartsch, recently described from off the northern coast of Puerto Rico.(1) Our present form is much larger and proportionately more attenuated. Bartsch mentions the presence of a tubercle at the base of the notch, a character which usually denotes adult growth and this would indicate that his species was fully adult. Besides being much larger, our present new form has a much straighter canal and columella than *johnsoni,* the wing-like expansions are also very much larger, proportionately, on the body whorl, and has only eight varices on last whorl.

---

(1) Smithsonian Misc. Collections, **91**, no. 2, p. 2, May 1934.

Bartsch proposed the genus *Eldridgea* with *E. johnsoni* as its type. The character, upon which his new genus was based, however, was that *johnsoni* carried the wing-like processes to an extreme point in development. Melville(1) selected *Strombus canicularis* Röding as the type of his subgenus *Tylotia,* which posesses similar alations and these are as fully developed as those exhibited by *johnsoni.* We figure a specimen of Röding's species (plate 29, fig. 4). *Tylotia* appears to us, however, to possess characters of generic value, and not limited, subgenerically to *Drillia.*

As the soft anatomy of *Aliceia* Daut. and Fisch. is still unknown, its position of course remains doubtful. If, however, it is found to be a Turritid, it may possibly replace *Tylotia.*

We have the pleasure of naming this species for Dr. José Cadenas, Rector of the University of Havana, in acknowledgment for his interest in the success of the Atlantis expedition.

Terebra evelynae new species

(PLATE 29, FIG. 1)

Description: Shell exceedingly slender, imperforate and solid. Whorls 25 remaining (loss of 5 whorls) almost flat and tapering to a very sharp summit. Color consisting of two broad bands of light brown with a narrow band of white at the whorl periphery. The bands of brown are somewhat blotched in a single adult specimen (holotype) though this color is evenly disposed in two of the smaller specimens. Spire slender and forming a very acute point. Angle of spire 7°. Aperture subovate, small and with the palatal edge slightly sinuous in profile. Parietal wall rather thickly glazed. Palatal lip simple with a rather deep notch (the canal) at the base. Columella thickened and inclined slightly. Sculpture on the early whorls of axial threads, slightly sinuous which on the later whorls becomes less pronounced and coalesces on the last few whorls as strong and irregular growth lines. Spiral threads are also present on the early whorls and though they persist they become less apparent on the later whorls. Subsutural depression rather pronounced on the early whorls which broadens and becomes less strong on the last four whorls. Suture slightly impressed.

---

(1) 1917, Proc. Malac. Soc. London 12, p. 160.

Length	*Width*	*Whorls*		
118	13.5 mm.	24 (incomplete)	Holotype	(M. C. Z.)
120.5	12.8 „	22 „	Paratype	(M. Poey)
75.1	9.1 „	19 „	„	(M. Poey)
54	6.8 „	21 (complete)	„	(M. C. Z.)

Holotype: Mus. Comp Zoöl. no. 135,077, *Atlantis* station no. 2981 (N. Lat. 22° 48′; W. Long. 78° 48′) off Northern Santa Clara Prov., Cuba, 225 fathoms. March 10, 1938. Two paratypes from the above locality and one each from *Atlantis* station no. 2999 (N. Lat. 23° 10′; W. Long. 81° 29′) off Matanzas, Cuba, 145-230 fathoms, March 17, 1938, and *Atlantis* station no. 2982-E (N. Lat 22° 45′; W. Long. 78° 45′) off Punta Alegre, Camagüey Province, Cuba, 150-180 fathoms, March 11, 1938.

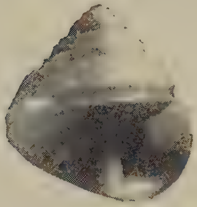
Remarks: A rather remarkable species because of its great length in relation to its width. It appears to be nearest *T. nassula* Dall, but differs in its much finer sculpture and proportionally, a much narrower shell for its length.

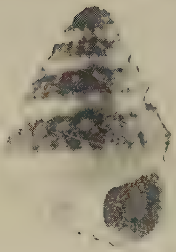
Cadulus (Gadila) iota nanus new subspecies

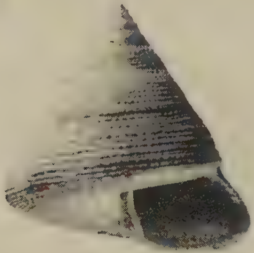
Description: Similar in size and general characters to the typical form, differing, however, in the flattened apical end which produces an elliptical orifice. It is also slightly smaller.

Length	*Width*	
1.8	0.5 mm.	Holotype

Holotype: Mus. Comp. Zoöl. no. 89,222, Gibara, Oriente Province, Cuba, 40 fathoms. C. G. Aguayo and P. J. Bermúdez collectors, september, 1937. A single paratype in the Museo Poey, Habana.


1


2


3

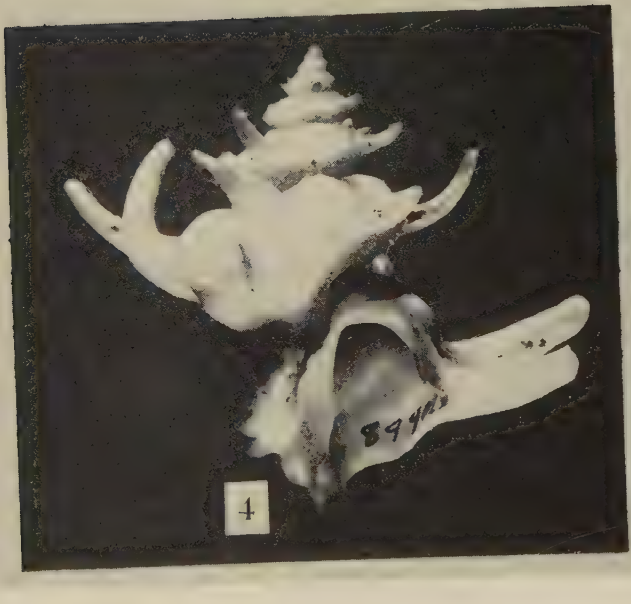


FIG. 1. *Solariella amabilis* Jeff. Cotype, 4 ×.
,, 2. *Solariella pourtalesi* Cl. and Ag. Holotype, 4 ×.
,. 3. *Calliostoma hassler* Cl. and Ag Holotype, nat. size.
,, 4. *Latiaxis juliae* Cl. and Ag. Holotype, about 2½ ×.

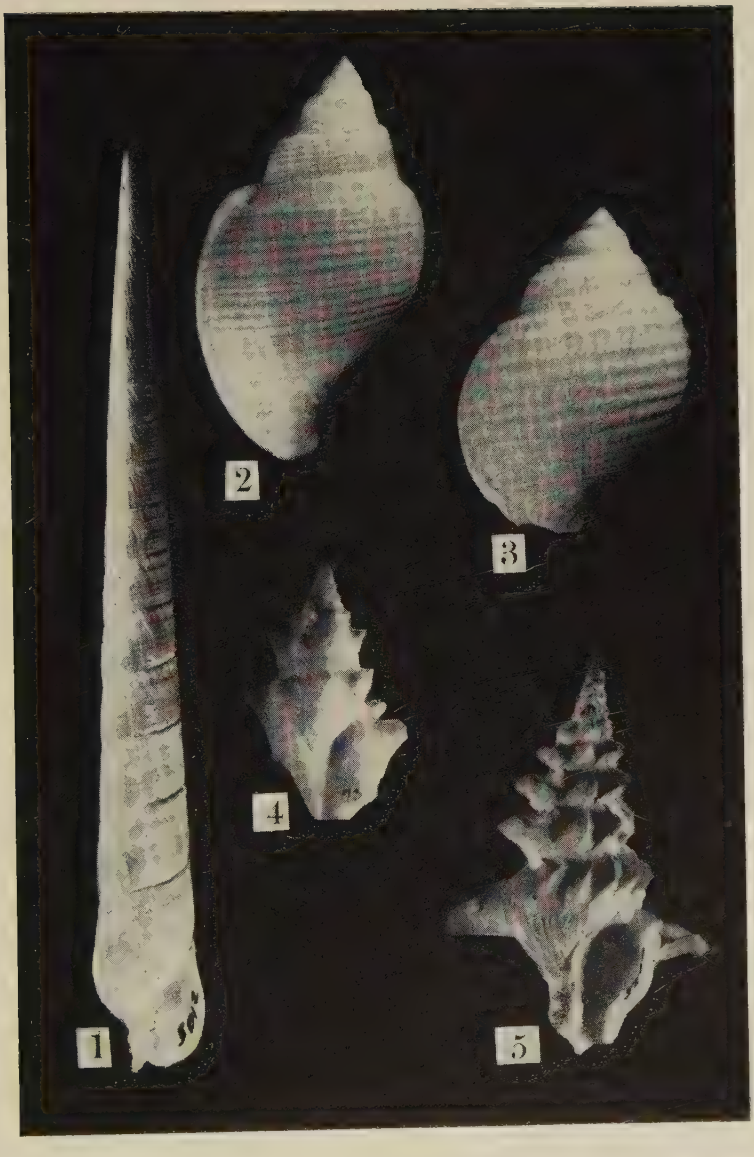


FIG. 1. *Terebra evelynae* Cl. and Ag. Holotype, nat. size.
" 2. *Oocorys barbouri* Cl. and Ag. Holotype, nat. size.
" 3. *Oocorys sulcata caribbaea* Cl. and Ag. Holotype, nat. size.
" 4. *Tylotia canicularis* Röding, nat. size.
" 5. *Tylotia cadenasi* Cl. and Ag. Holotype, nat. size.

Contribution No. 225

Vol. XIII ABRIL 15, 1939. Núm 2

MEMORIAS
DE LA
SOCIEDAD CUBANA DE HISTORIA NATURAL
"FELIPE POEY"

RESULTADOS DE LA PRIMERA EXPEDICION EN LAS ANTILLAS DEL KETCH ATLANTIS BAJO LOS AUSPICIOS DE LAS UNIVERSIDADES DE HARVARD Y HABANA

Foraminíferos del Género Recurvoides, descripción de una Especie Nueva.

POR PEDRO J. BERMÚDEZ
Museo Poey, Universidad de la Habana.

El género *Recurvoides* Earland, de la familia *Lituolidae*, está representado por un corto número de especies que habitan preferentemente los fondos profundos de los mares actuales.

Las especies conocidas hasta hoy son cuatro, incluyendo una nueva:

Recurvoides contortus Earland
Recurvoides obsoletus (Goës)
Recurvoides turbinatus (H. B. Brady)
Recurvoides clenchi Bermúdez n. sp.

Estos interesantes Foraminíferos arenáceos muestran relaciones con el género *Haplophragmoides* Cushman, pero difiere de él, según puede verse en la descripción, porque las cámaras están colocadas en series planispirales, abrazándose parcialmente, estando el eje de vuelta de la segunda serie aproximadamente en ángulo recto a la primera, mientras que *Haplophragmoides* presenta una concha con crecimiento típicamente distinto.

Contribution No. 225 of the
Woods Hole Oceanographic Institution

Las colecciones hechas a bordo del Atlantis a principios de 1938 fueron muy prolíferas, habiéndose obtenido preciosas series de Foraminíferos del género *Recurvoides.* Todas las especies fueron encontradas excepto la primera *R. contortus* Earland, que a pesar de haber sido reportada para las Antillas por el propio Earland, considerando las ilustraciones de Flint(1) como pertenecientes a su especie, no ha aparecido en nuestro material.

Seguidamente se hace un estudio de las tres especies que tenemos del género. Todas se han situado en las colecciones del Museo de Zoología Comparada de Harvard y Museo Poey, Universidad de la Habana.

Género RECURVOIDES Earland, 1934

Genoholotipo *Recurvoides contortus* Earland, 1934, Discovery Reports, Foraminífera of the Falklands Sector of the Antartic. (Excluding South Georgia), vol. 10, pp. 91, 92, pl. 10, figs. 7-19.

Concha libre, arenácea, compuesta de muchas vueltas, cada una con muchas cámaras. Las cámaras están colocadas en dos series planispirales, abrazándose parcialmente, estando el eje de vuelta de la segunda serie aproximadamente en ángulo recto a la primera, por lo tanto la segunda serie cubre la primera, pero deja visible en una de las caras, el borde periférico de la vuelta final como una fuerte línea de cámaras, extendiéndose a través de la porción umbilical de la concha adulta; pared formada de granos de arena de tamaño variable, con una cantidad considerable de cemento ferruginoso; abertura pequeña, sobre la cara final de la última cámara, algunas veces con un labio protáctil.

RECURVOIDES OBSOLETUS (Goës)

(LÁM. 5, FIGS. 1-3)

Haplophragmoides obsoletum Goës, 1896, Bull. Mus. Comp. Zool., vol. 29, no. 1, p. 31, pl. 3, figs. 14-16.

Concha biconvexa, ligeramente comprimida, fuerte, contorno periférico circular; última vuelta de espira formada de seis u ocho cámaras, suturas borradas, cuando se humedecen los ejemplares se hacen visibles, nunca son profundas, cámaras planas; pared fuertemente arenácea, formada de granos fuertes de arena amarillenta o ferruginoso-pálido, con fragmentos cortos de espículas, con terminado más o menos uniforme; borde de la concha fuertemente redondeado;

---

(1) *Haplophragmoides scitulus* Flint (no H. B. Brady), 1879 (1899), Rept. U. S. Nat. Mus., p. 276, pl. 20, fig. 2.

ombligo cubierto por una lámina de material de la concha; abertura redondeada o algo alargada y encorvada con un reborde saliente o protáctil.

Diámetro 1-2 mm.

El Holotipo procede del Mar Caribe dragado entre 382-1630 brazas de profundidad, reportado como escaso. Esta interesante especie fué reportada por primera vez por Goës procedente del Mar Caribe, una de las estaciones de donde la obtuvo fué 23 millas S.S.E. de Port Royal Jamaica (Lat. 17° 36′ N. Long. 76° 46′ W.) 966 brazas de profundidad (Albatros Sta. 2140). Cushman la consideró sinónimo de *Recurvoides turbinatus* (H. B. Brady),(1) no obstante el estudio comparativo de ambas especies y el haberlas podido separar estudiando la estructura externa e interna de grandes series de ejemplares adultos, me ha llevado a la convicción de que *Recurvoides obsoletus* es una especie distinta que merece ser restablecida. La figura de *Trochammina turbinata* dada por Cushman muestra claramente una especie umbilicada o semiumbilicada mientras que las ilustraciones de Goës corresponden a una especie púdica y con más cámaras.

La descripción dada por Goës identifica la especie, las figuras aunque algo crudas, ayudan a reconocer la forma; parece que el ejemplar seleccionado para los dibujos era imperfecto, faltándole la abertura y parte del tabique de la cara apertural en la última cámara; los demás caracteres, el número de cámaras, dimensiones y la forma están muy correctamente representados, especialmente en la figura 16 de la cara dorsal.

Se ha encontrado frecuente en el material dragado por el Atlantis, las localidades donde fué obtenida la presente especie son las siguients:

Atlantis Stas.

2952.	Lat. 21° 52′	N.	Long. 85° 00′	W.	570	brazas	de	profundidad.
2953.	Lat. 21° 47′ 30″	N.	Long. 84° 32′ 30″	W.	615	„	„	„
2967B.	Lat. 19° 43′ 30″	N.	Long. 74° 57′ 30″	W.	1425	„	„	„
2988.	Lat. 23° 15′	N.	Long. 79° 57′	W.	380	„	„	„
2993.	Lat. 23° 24′	N.	Long. 80° 44′	W.	580	„	„	„

---

(1) Cushman, J. A., 1920, U. S. Nat. Mus., Bull. 104, pt. 2, p. 81.

RECURVOIDES TURBINATUS (H. B. Brady)

(LÁM. 5, FIGS. 4-6)

Haplophragmoides turbinatum H. B. Brady, 1884, Report. Voy. Challenger, Zoology, Vol. 9, p. 312, pl. 35, figs. 9a-c.

Trochammina turbinata Cushman, 1920, U. S. Nat. Mus., Bull. 104, pt. 2, p. 81, pl. 17, fig. 2.

Concha en espiral, primera porción regular, subglobulosa o deprimida, formada de dos circunvoluciones oblicuas o irregulares, contorno periférico circular; cinco o seis cámaras en la última vuelta de espira, cámaras planas separadas por suturas poco discernibles; pared gruesa, fuertemente arenácea, constituída por granos de arena de color ferruginoso, más pálido en las suturas de las cámaras; ombligo descubierto y poco visible; abertura en la cara terminal de la última cámara, como una hendidura alargada y provista de un labio poco protáctil.

Dimensiones 0.75-1.50 mm.

Los ejemplares originalmente descritos por Brady fueron obtenidos por el Challenger (Sta. 346) en 2350 brazas de profundidad en el Océano Atlántico, al Sur de la línea ecuatorial, hacia la costa Oeste del Africa. En adición hay una serie de records del Challenger y del Albatross, todos de grandes profundidades. Cushman lo reportó de numerosas estaciones del Golfo de México con un average de más de 1500 brazas. Es una especie de aguas profundas con una gran área de dispersión.

Los ejemplares estudiados por el autor proceden de la estación del Atlantis 2966. Mar Caribe, Sur de Cuba (Lat. 20° 47′ 5″ N. Long. 80° 24′ 5″ W.) en 2125 brazas de profundidad.

Recurvoides clenchi Bermúdez n. sp.

(LÁM. 5, FIGS. 7-9)

Concha biconvexa, algo comprimida, de aspecto fuerte, contorno periférico irregularmente lobulado, última vuelta de espira formada de ocho cámaras lobuladas, suturas marcadas por fuertes depresiones en el borde periférico, el resto de la sutura poco visible, cámaras globosas; pared fuertemente arenácea, gruesa, con gran cantidad de arena fina, amarillenta o ferruginosa y con espículas largas colocadas con irregularidad en toda la concha, carácter que unido con el aspecto grotesco de la concha la distingue fácilmente; ombligo cubierto por una lámina de material arenáceo; abertura redondeada, protegida de un labio saliente, colocada en el centro de la cara apertural de la última cámara.

Dimensiones 1-2 mm.

Holotipo en la colección Cushman, Sharon, Mass., procedente de Atlantis Sta. 2953 (Lat. 21° 47′ 30″ N. Long. 84° 32′ 30″ W.) 615 brazas de profundidad, Sur de Bahía Corrientes, Sur de Cuba.

Además fué obtenido en Atlantis Sta. 2954 que está en la misma área en 900 brazas de profundidad.

Esta especie nueva es más próxima a *Recurvoides obsoletus* (Goës), con el que se encuentra algunas veces mezclado.

Nombrada en honor del Sr. William J. Clench, Curator of Mollusks en el Museo de Zoología Comparada de la Universidad de Harvard, Cambridge, Mass.

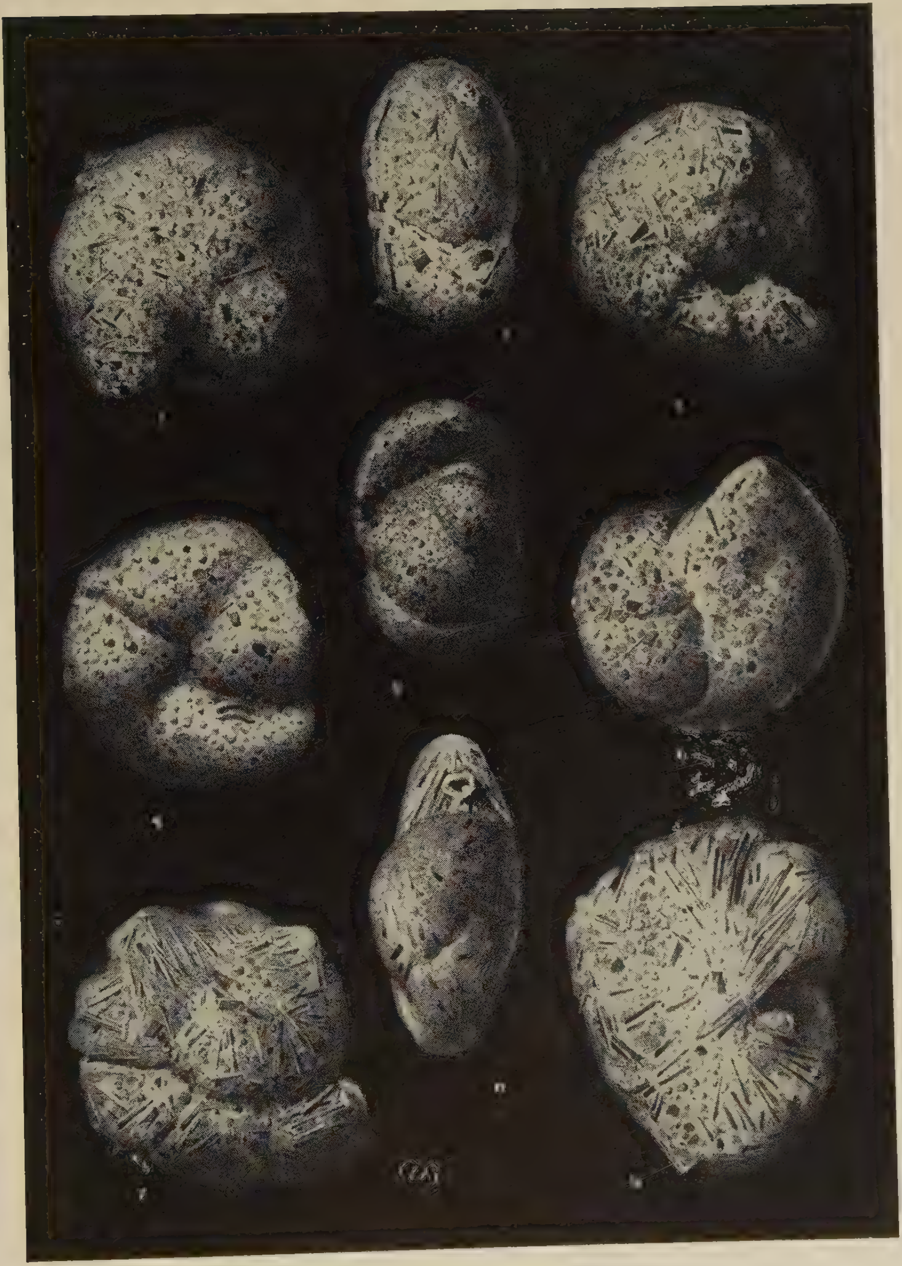
Las especies ilustradas en este trabajo se han depositado en la Colección del Dr. J. A. Cushman, Sharon, Mass. Una buena serie representando todas las especies ha sido situada en el Museo de Zoología Comparada de la Universidad de Harvard, Museo Poey, Universidad de la Habana, y en las colecciones privadas de Mrs. D. K. Palmer y del autor.

LAMINA 5

FIGS. 1-3. *Recurvoides obsoletus* (Goës) × 20.
Atlantis Sta. 2952 (Lat. 21° 52′ 00″ N. Long. 85° 00′ W.)
570 brazas de profundidad.
Fig. 1, vista dorsal; 2, vista apertural; 3, vista ventral.

„ 4-6. *Recurvoides turbinatus* (H. B. Brady) × 40.
Atlantis Sta. 2966 (Lat. 20° 47′ 05″ N. Long. 80° 24′ 05″ W.)
2125 brazas de profundidad.
Fig. 4, vista ventral; 5, vista apertural; 6, vista dorsal.

, 7-9. *Recurvoides clenchi* Bermúdez n. sp. × 25.
Atlantis Sta. 2953 (Lat. 21° 47′ 30″ N. Long. 84° 32′ 30″ W.)
615 brazas de profundidad.
Fig. 7, Holotipo, vista dorsal; 8, vista apertural; 9, vista ventral.



BERMÚDEZ: Foraminíferos del género *Recurvoides.*

Contribution No. 227

Daily Temperature Variations in the Western North Atlantic.

By

H. R. Seiwell.[1][2]

IN the summers of 1936, 1937, and 1938 continuous measurements of temperature (and other characteristics) at fixed depths (between surface and 1200—1300 metres), over intervals of 57 to 314 hours, have shown that disturbances of the water column cause significant short period changes in the observed state of the sea. Thus, in general, projections of oceanographic characteristics, based on isolated series of samplings, will not represent average conditions (for the observation period) unless observational data is controlled by ascertaining orbits of time variation for estimation of significance of calculated orbits of space variation.

Station Data.

Stations for measurement of time variations of temperature (and other oceanographic characteristics) were located in the western Atlantic basin between Bermuda and the Gulf Stream system, where for considerable distances, horizontal gradients of oceanographic properties are small (in projected oceanographic sections the isolines maintain relatively level positions), a condition necessary because the ship was not anchored. During operation, frequent observations of ship's drift (and favourable weather) enabled samplings generally to be made within a radius of 2—3 miles (in no case exceeding 5 miles) from the mean station positions tabulated in Table 1. Mean geographic positions of stations 2887 and 3091 are nearly identical, both being located about 110 miles north-

---

[1] Assistance for reduction of these observations was supported by a grant from the Penrose Fund of the American Philosophical Society.

[2] Contribution No. 227 from the Woods Hole Oceanographic Institution.

Table 1.

Station	λ	φ	Measured depth	Duration of sampling 60° time	Number samplings
2639	66°25′W	35°07′N	5130	9^h 57′ July 9 — 17^h 07′ July 13, 1936	24
2886	65°59′W	32°19′N	4830	23^h 46′ June 16 — 08^h 28′ June 19, 1937	50
2887	65°56′W	34°01′N	5216	23^h 16′ June 19 — 13^h 34′ June 22, 1937	41
				7^h 57′ June 24 — 08^h 24′ June 28, 1937	72
3091	65°54′W	34°02′N	5133	12^h 21′ June 16 — 14^h 22′ June 29, 1938	194

west of Bermuda; station 2886 (about 100 miles to the south) is approximately 60 miles west of Bermuda. The present discussion concerns only these three stations; results from station 2639 having been discussed previously[3]).

To reduce observations for analysis, individual temperature depth curves for each sampling were scaled both for depths of significant isotherms and for temperature at standard depths, the scaled items being consolidated into averages, or used individually as required. The density distributions at each station were determined by combining average temperatures at standard depths and average depths of standard isotherms with salinity values scaled from temperature salinity relationships.

Vertical Displacements of Isotherms.

To specify vertical displacements at particular depths in the water column reference is made to various isotherms (average depths tabulated in Table 2), the apparent changes in position of which (in the western Sargasso Sea) may be considered as resulting from vertical oscillations of the water particles, a circumstance deduced because of the small horizontal isothermal gradients[4]). Certain errors affecting the items of each sampling, due to the slow drift of the ship and to the eddying motion of the water, are largely eliminated by averaging.

Although ranges of vertical displacements of isotherms vary from day to day (Table 2) a definite relationship to the vertical density distribution ($\Delta\sigma_t/\Delta Z$) always exists. Thus, at stations 2887 (Fig. 1) and 3091 (Fig. 2) magnitudes of vertical displacements, at a maximum where the water is least stable (to depths of 1200—1300 m.; $\Delta\sigma_t/\Delta Z =$ approximately 2×10^{-4}), are suppressed with increasing stratification.

---

[3]) See "Short period vertical oscillations in the western basin of the North Atlantic." Papers in Physical Oceanography and Meteorology. Vol. V, No. 2, 1937.

[4]) Maximum gradient of 10° isotherm: 1.33 metres per kilometre; and of 17° isotherm: 1.00 metres per kilometre; see footnote 2.

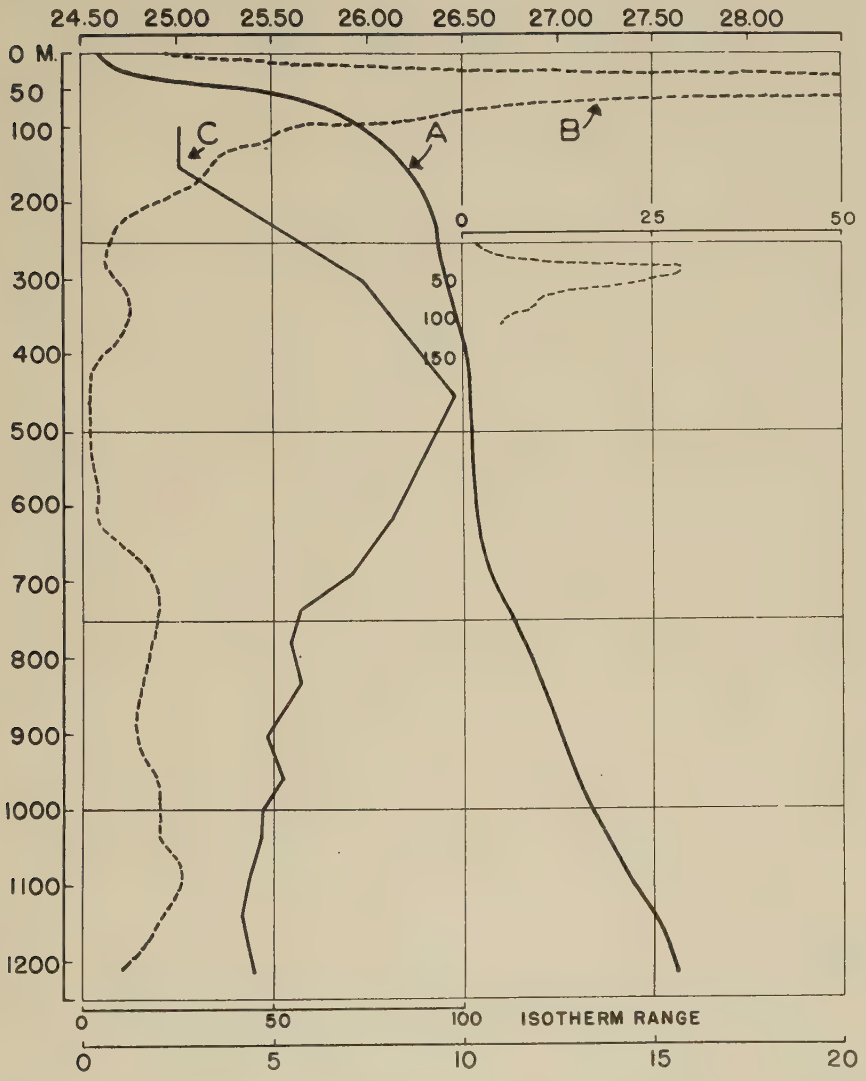


Fig. 1. A = average vertical distribution of density, σ_t, (top scale); B = average vertical variation of density, $\Delta\sigma_t/\Delta Z \times 10^3$ (lower scale); C = average vertical displacement ranges of isotherms (20°—6°; Table 2) for 6 days, Station 2887.

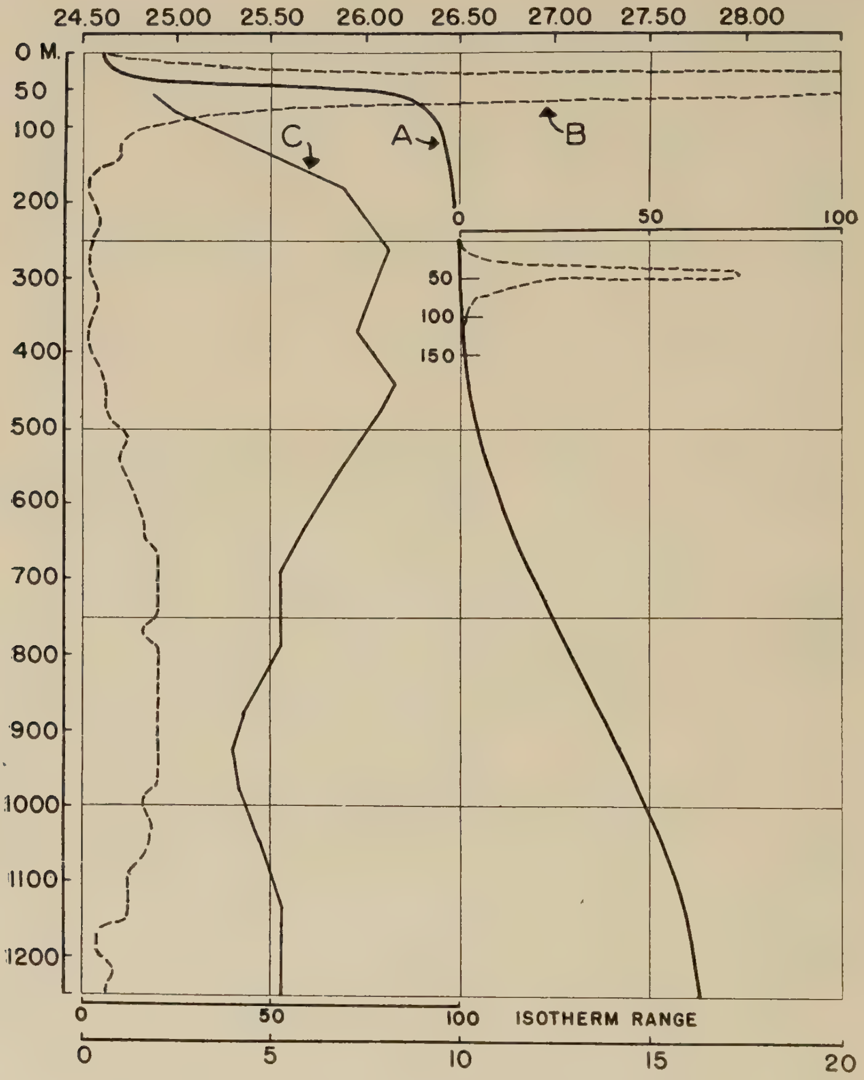


Fig. 2. A = average vertical distribution of density, σ_t, (top scale); B = average vertical variation of density, $\Delta\sigma_t/\Delta Z \times 10^3$ (lower scale); C = average vertical displacement ranges of isotherms (20°—5°; Table 2) for 13 days, Station 3091.

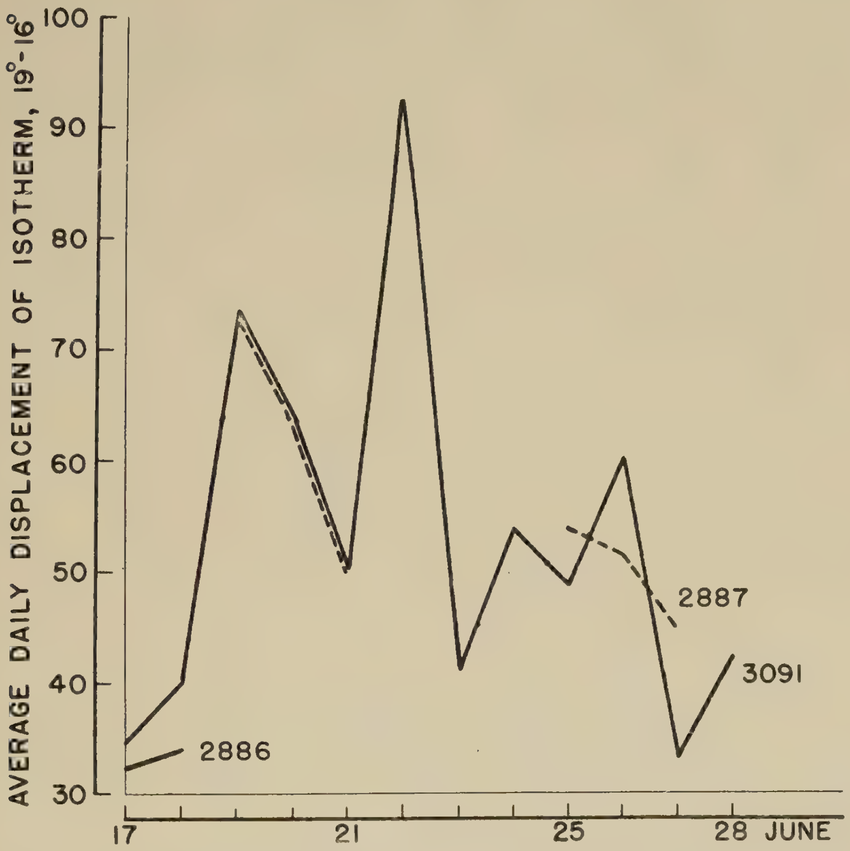


Fig. 3. Average daily vertical displacements of all unit isotherms between 19° and 6° for Stations 2886 (2 days) and 2887 (6 days), in 1937 and Station 3091 (13 days) in 1938 (see Table 1).

In this least stratified water, between 17° and 18° isotherms[5]), average daily vertical displacements at station 2887 were 81 to 97 m. and at station 3091, 73 to 83 m.; in the intermediately stratified deep water ($\Delta\sigma_t/\Delta Z = 2{\cdot}6 \times 10^{-3}$), average daily ranges of isotherms (15°—6°) decreased to 42—57 m. at station 2887 and to 40—59 m. at station 3091; and in the strongly stratified surface layer ($\Delta\sigma_t/\Delta Z = 74 \times 10^{-3}$)

---

[5]) At both stations the least stratified water was bounded by the 17° and 18° isotherms, and although observations were made at identical dates on successive years (Table 1) their average depths differed respectively by 121 and 142 metres, thus:

		Depth	$\frac{\Delta\sigma_t}{\Delta Z} \times 10^3$	σ_t
Station 2887	18°	300	0·2—1·2	26·41
	17°	618		26·57
Station 3091	18°	179	0·2—0·6	26·46
	17°	476		26·56

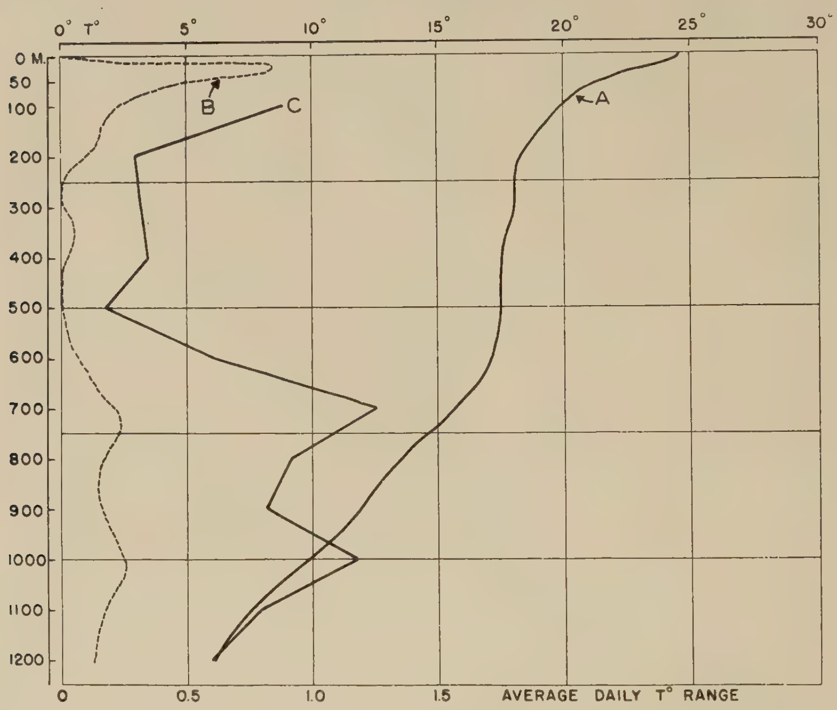


Fig. 4. A = average vertical temperature distribution (top scale); B = average vertical variation of temperature, $\Delta T^{\circ}/\Delta Z \times 10^2$ (top scale); C = average daily temperature ranges at standard depths (lower scale; Table 5) for 6 days at Station 2887.

average daily ranges of isotherms (20° and 19°) were reduced to 19—26 m. (Table 2).

The occurrence of large day-by-day variations in magnitude of vertical displacements of identical isotherms is brought out by comparison of minimum and maximum daily ranges[6]) for 5 days at station 2887 and 12 days at station 3091 (Table 2). Likewise, day-by-day variations in average daily vertical displacements for all unit isotherms between 19° and 6°, at station 3091 (Fig. 3) during 12 days, show that the water column was disturbed least on June 27 and most on June 22, the average vertical displacements on the latter date being nearly three times that on the former.

Total changes in depths of isotherms (20°—6°) in the western North Atlantic (Table 3) during 5 consecutive days at station 2887 and 12 consecutive days at station 3091, far exceed maximum displacements recorded for any individual day (Table 2); at the former station, total displacements up to 165 m. occurred in the least stable water (between

---

[6]) In this respect, the computed daily ranges, being subjected to randomness of the observations, are not for any one case an accurate basis for comparison; the average range, used above, is a better statistic for characterization of the data.

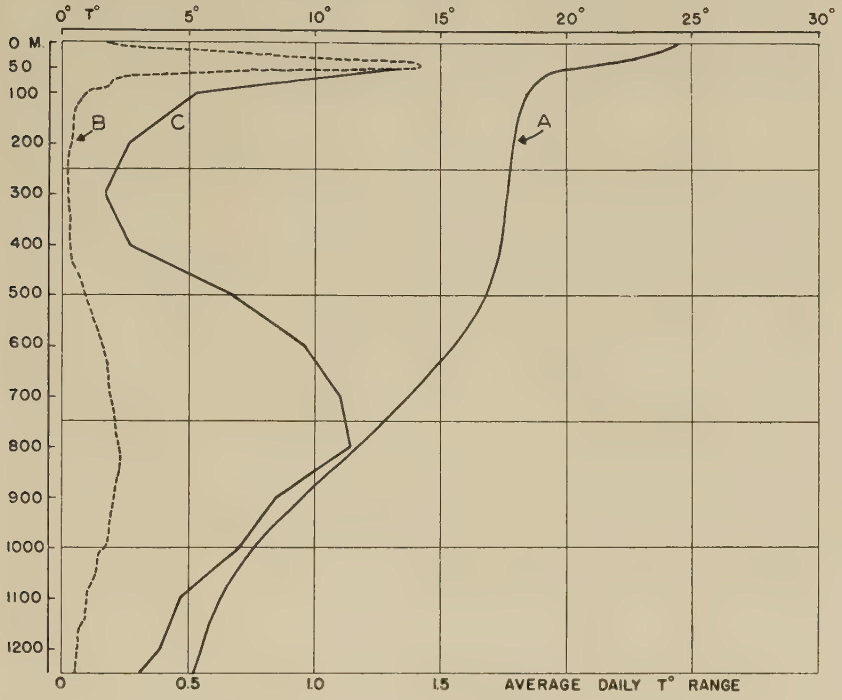


Fig. 5. A = average vertical temperature distribution (top scale); B = average vertical variation of temperature, $\Delta T^\circ / \Delta Z \times 10^2$ (top scale); C = average daily temperature ranges at standard depths (lower scale, Table 5) for 13 days at Station 3091.

17° and 18°), between 74—129 m. in the underlying intermediately stable water, and between 39—41 m. in the overlying highly stable water; whereas, at the latter station, corresponding values were 227 m., 144—172 m. and 38—82 m. These large vertical displacements result from short-period vertical oscillations of 24 lunar hours or less, superimposed on longer period trends; characterizations of the latter, obtained by fitting straight lines to the 12 daily average depths of each isotherm at station 3091, and determining (by the method of least squares) the coefficients *a* and *b* of the general equation

$$y = a + bx,$$

are given in Table 4. The coefficient *b* denoting the daily change in average depth of individual isotherms, shows a pronounced relationship to vertical variation of density. In the surface layer, between 20·0° and 17·75°, the downward slope of isotherms increased from 0·59 to 9·77 m. per day; in the least stratified part of the water column, between 17·75° and 17·50°, there occurred an abrupt reversal of slope, and slightly deeper, the trend of the 17·0° isotherm sloped upward at an average rate of 6·26 m. per day. In still deeper water, with increasing stability, isothermal slopes continued upward, but at a

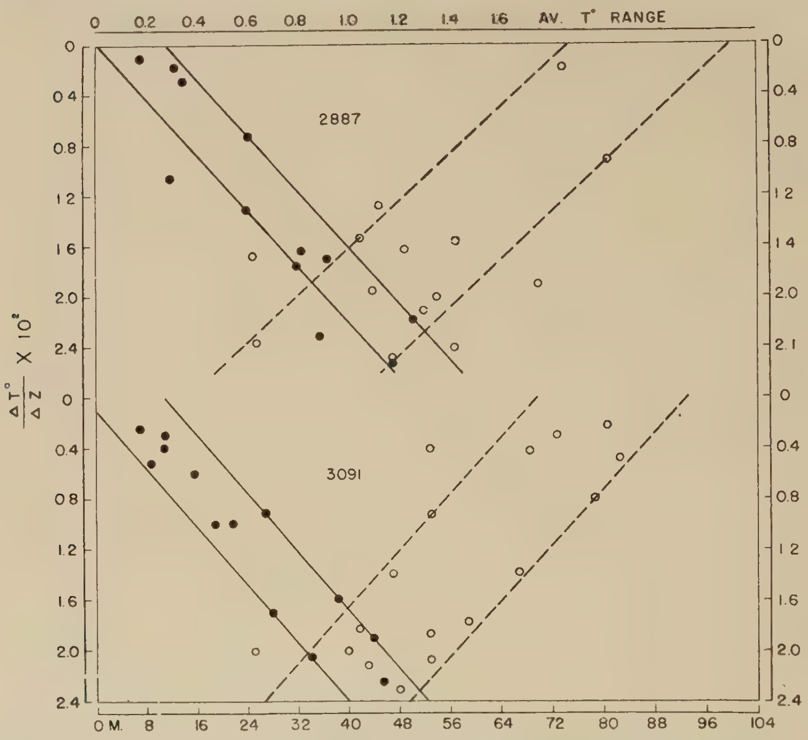


Fig. 6. Relationship of average daily temperature ranges at standard depths (closed circles) and average daily displacement ranges of isotherms (open circles) to average vertical variation of temperature, $\Delta T^\circ/\Delta Z \times 10^2$, for Stations 2887 and 3091 (Tables 2 and 5).

slower rate; at 6° the linear rate was reduced to 3·07 m. per day. Thus, because of the abrupt phase reversal between 17° and 18° isotherms the average vertical distance between them increased from 227 m. on June 17 to 367 m. on June 28; above 17·5° the water became increasingly warmer and below (to 1200 m.) increasingly colder.

Temperature Variations at Standard Depths.

Daily ranges of temperature are larger at depths where thermal stratification is greatest, a circumstance brought out for stations 2886, 2887, and 3091 by Tables 5 and 6 and Figures 4 and 5. Conditions at all three stations are essentially similar, and, as illustrated for the two latter, changes in magnitude of average daily temperature ranges are sensitive to small variations in thermal stratification. The interdependence of average daily temperature ranges and average vertical displacements of the water column, and their contrary relation to thermal stratification (Fig. 6) indicate that the damping effect of stratification on vertical displacement is insufficient to offset increased values of the former occurring with increased stratification. Thus, at stations 2887 and 3091, between the 17° and 18° isotherms, where temperature (like density) changes slowly with depth, $\Delta T°/\Delta Z = 0{\cdot}06° \times 10^{-2}$ to $0{\cdot}9 \times 10^{-2}$, average daily temperature ranges were as low as 0·17°; in the overlying surface layer (in the vicinity of 20°—21° where $\Delta T°/\Delta Z$ attains values up to $14{\cdot}2 \times 10^{-2}$) average daily temperature ranges were up to 1·35°, while in the intermediately stratified deeper water (between 17° and 6° maximum, values of $\Delta T°/\Delta Z = 2{\cdot}3 \times 10^{-2}$ to $2{\cdot}5 \times 10^{-2}$ average daily temperature were ranges up to 1·26° (Table 5).

Comparisons of maximum and minimum daily temperature ranges (Table 6) show large day-by-day variations at identical depths, a condition inferred from the nature of daily variations in magnitudes of vertical displacements (Fig. 3). Likewise, the total temperature ranges at standard depths for the various observation periods considered are significantly large; during 12 days at station 3091 the smallest variation of 0·50° occurred in the least stratified water, and the largest of 3·52° in the deeper, more strongly stratified water (Table 6).

As a result of the previous discussion it is to be expected there will be a day-by-day change in average temperatures at standard depths, and, as illustrated for 5- and 12-day periods at station 2887 and 3091 (Table 7), the variation of average daily temperatures is smallest for depths characterized by least thermal stratification (0·04°—0·25°), and greatest (1·13°—1·28°) in the intermediately stratified water at mid-depths.

Summary.

In the waters of the western Sargasso Sea, as represented by "Atlantis" stations 2886, 2887, and 3091, continuous temperature measurements at fixed depths (to 1200—1300 m.) over time intervals up to 12 days, show average daily vertical displacements of the water particles of 24 to 97 m. and total displacements of 38 to 227 m., the larger values occurring where the water is least stable; with increasing stratification vertical motions of the water particles are damped. As a result of this phenomenon, temperature at fixed depths (for all 3 stations) showed an average daily range of 0·08° to 1·35°, and a total range for the 13-day period (station 3091) of 0·50° to 3·44°.

(Tables 2—7: see following pages)

Table 2.

Isotherm	Station 2886		Station 2887				Station 3091			
	Average depth	Average daily range	Average depth	Average daily range	Minimum daily range	Maximum daily range	Average depth	Average daily range	Minimum daily range	Maximum daily range
20·0°	—	—	98	26	21	23	56	19	5	28
19·0°	84	40	150	25	12	35	79	25	11	55
18·0°	288	54	300	74	57	94	179	69	29	107
17·75°	—	—	—	—	—	—	260	81	40	106
17·5°	393	49	449	97	36	161	367	73	34	116
17·25°	—	—	—	—	—	—	438	83	39	142
17·0°	482	36	618	81	43	117	476	79	42	149
16·0°	567	30	687	70	51	97	566	67	27	144
15·0°	625	24	733	57	39	80	631	59	26	120
14·0°	676	29	776	54	27	74	686	53	24	103
13·0°	725	38	829	57	27	85	737	53	30	108
12·0°	772	32	899	49	41	67	784	53	30	110
11·0°	814	25	954	52	47	61	829	48	30	110
10·0°	856	29	995	47	39	59	873	43	21	111
9·0°	901	31	1035	47	34	62	921	40	18	106
8·0°	953	21	1079	44	28	63	974	42	18	103
7·0°	1012	30	1135	42	33	58	1039	47	21	101
6·0°	1085	46	1211	45	34	69	1131	53	24	110
5·0°	1241	48	—	—	—	—	1293	53	27	85

Table 3.

Isotherm	Station 2887			Station 3091		
	Minimum depth	Maximum depth	Total displacement	Minimum depth	Maximum depth	Total displacement
20·0°	80	119	39	42	80	38
19·0°	127	168	41	49	131	82
18·0°	236	360	124	95	291	196
17·75°	—	—	—	159	386	227
17·50°	335	500	165	296	466	170
17·25°	—	—	—	375	534	159
17·0°	542	673	131	403	575	172
16·0°	631	760	129	496	668	172
15·0°	692	807	115	558	714	156
14·0°	736	853	117	608	752	144
13·0°	781	893	112	652	797	145
12·0°	839	937	98	695	850	155
11·0°	883	1000	117	738	910	172
10·0°	927	1033	106	780	950	170
9·0°	971	1069	98	831	993	162
8·0°	1021	1117	96	882	1039	157
7·0°	1091	1172	81	948	1120	172
6·0°	1176	1250	74	1032	1200	168
5·0°	—	—	—	1232	1354	122

Table 4.

Isotherm	Station 3091 $y - a + bx$		Average depth June 17	Average depth June 28
	a	b		
20·0°	59·26	—0·59	56·2	50·1
19·0°	88·05	—1·37	83·3	67·9
18·0°	235·30	—8·39	200·6	139·0
17·75°	324·16	—9·77	282·1	212·2
17·50°	360·97	0·85	345·2	386·0
17·25°	402·40	5·28	394·0	469·3
17·0°	433·61	6·26	427·4	506·1
16·0°	530·41	5·38	525·3	592·5
15·0°	598·58	4·82	596·5	657·9
14·0°	653·81	4·86	653·6	714·5
13·0°	705·00	4·77	706·8	765·4
12·0°	752·80	4·60	755·2	809·4
11·0°	799·71	4·28	802·5	851·3
10·0°	845·67	4·08	849·3	895·1
9·0°	894·26	3·89	898·7	941·6
8·0°	949·11	3·59	954·2	994·5
7·0°	1013·63	3·67	1016·7	1058·6
6·0°	1109·57	3·07	1110·1	1152·9
5·0°	1269·71	3·65	1288·9	1328·4

Table 5.

	Station 2886		Station 2887		Station 3091	
Depth	Average temperature	Daily average temperature range	Average temperature	Daily average temperature range	Average temperature	Daily average temperature range
0	25·22°	—	24·55°	—	24·34°	—
50	—	—	—	—	20·08°	1·35°
100	18·71°	0·64°	19·92°	0·89°	18·44°	0·54°
200	18·17°	0·08°	18·27°	0·30°	17·91°	0·27°
300	17·99°	0·18°	18·02°	0·32°	17·67°	0·17°
400	17·46°	0·13°	17·53°	0·35°	17·38°	0·27°
500	16·83°	0·31°	17·46°	0·18°	16·78°	0·67°
600	15·48°	0·47°	17·13°	0·61°	15·51°	0·96°
700	13·51°	0·63°	15·74°	1·26°	13·73°	1·10°
800	11·35°	0·65°	13·56°	0·92°	11·65°	1·14°
900	9·03°	0·65°	11·96°	0·82°	9·44°	0·85°
1000	7·19°	0·46°	9·90°	1·18°	7·56°	0·70°
1100	5·87°	0·40°	7·61°	0·80°	6·28°	0·47°
1200	5·19°	0·25°	6·13°	0·60°	5·50°	0·39°
1300	—	—	—	—	4·99°	0·22°

Table 6.

Station 2886

Depth	Minimum temperature	Maximum temperature	Total range	Minimum daily range	Maximum daily range
0	—	—	—	—	—
50	—	—	—	—	—
100	18·25°	18·99°	0·74°	0·59°	0·69°
200	18·12°	18·20°	0·08°	0·07°	0·08°
300	17·88°	18·07°	0·19°	0·17°	0·19°
400	17·39°	17·52°	0·13°	0·13°	0·13°
500	16·64°	17·03°	0·39°	0·30°	0·31°
600	15·19°	15·77°	0·58°	0·47°	0·47°
700	13·11°	13·87°	0·76°	0·62°	0·64°
800	11·04°	11·75°	0·71°	0·60°	0·69°
900	8·79°	9·48°	0·69°	0·60°	0·69°
1000	6·86°	7·51°	0·65°	0·27°	0·65°
1100	5·65°	6·06°	0·41°	0·38°	0·41°
1200	5·02°	5·30°	0·28°	0·21°	0·28°
1300	—	—	—	—	—

Station 2887

Depth	Minimum temperature	Maximum temperature	Total range	Minimum daily range	Maximum daily range
0	—	—	—	—	—
50	—	—	—	—	—
100	19·00°	21·03°	2·03°	0·57°	1·42°
200	18·17°	18·96°	0·79°	0·18°	0·32°
300	17·70°	18·20°	0·50°	0·16°	0·42°
400	17·00°	17·80°	0·80°	0·10°	0·55°
500	16·94°	17·50°	0·56°	0·04°	0·55°
600	16·47°	17·42°	0·95°	0·24°	0·93°
700	14·84°	16·77°	1·93°	0·63°	1·71°
800	12·82°	15·15°	2·33°	0·36°	1·53°
900	10·60°	12·80°	2·20°	0·45°	1·51°
1000	8·29°	11·00°	2·71°	0·94°	1·39°
1100	6·83°	8·35°	1·52°	0·64°	1·11°
1200	5·77°	6·90°	1·13°	0·27°	1·10°
1300	—	—	—	—	—

Station 3091

Depth	Minimum temperature	Maximum tempetature	Total range	Minimum daily range	Maximum daily range
0	—	—	—	—	—
50	19·00°	22·05°	3·05°	0·90°	2·20°
100	17·95°	19·38°	1·43°	0·22°	1·01°
200	17·65°	18·43°	0·78°	0·08°	0·77°
300	17·48°	17·98°	0·50°	0·06°	0·26°
400	17·04°	17·70°	0·66°	0·15°	0·51°
500	15·96°	17·37°	1·41°	0·34°	1·09°
600	14·19°	16·85°	2·66°	0·36°	1·95°
700	11·88°	15·32°	3·44°	0·47°	2·33°
800	9·61°	12·97°	3·36°	0·73°	2·50°
900	7·73°	11·25°	3·52°	0·38°	2·08°
1000	6·32°	8·85°	2·53°	0·35°	1·45°
1100	5·50°	7·20°	1·70°	0·24°	1·06°
1200	5·15°	6·00°	0·85°	0·22°	0·67°
1300	4·74°	5·27°	0·53°	0·11°	0·31°

Table 7.

Depth	Range of average daily temperature	
	Station 2887	Station 3091
	5 days	12 days
50	—	1·01°
100	0·35°	0·76°
200	0·13°	0·37°
300	0·18°	0·25°
400	0·12°	0·27°
500	0·04°	0·94°
600	0·30°	1·23°
700	1·02°	1·18°
800	1·13°	1·28°
900	0·64°	1·24°
1000	1·12°	0·98°
1100	0·54°	0·52°
1200	0·28°	0·38°
1300	—	0·29°

Contribution No. 228

[Reprinted from the Journal of the American Chemical Society, **61**, 2806 (1939).]

[Contribution No. 228 from the Woods Hole Oceanographic Institution]

The Helium–Neon Content of Sea Water and its Relation to the Oxygen Content[1]

By Norris W. Rakestraw, Clifford E. Herrick, Jr.,[2] and Wm. D. Urry

One of the most widely discussed topics in the field of oceanography at the present time is the cause and significance of the "oxygen minimum zone." The vertical distribution of oxygen in the deeper parts of the ocean shows a minimum concentration at a depth which varies with the location, generally between 200 and 1000 meters. This minimum may be very pronounced, as in parts of the Pacific where there is virtually no oxygen. In the Atlantic the minimum zone is seldom less than 30% saturated, and in the far north and south there is sometimes no minimum.

Some time ago there were reported analyses of the helium–neon content of sea water,[3] the outstanding feature of which was an apparent minimum of the helium–neon mixture coinciding with the oxygen minimum in the same water. The significance of this was discussed briefly and some possible explanations suggested. All of these explanations, however, are in rather serious conflict with other oceanographic evidence. In view of this, as well as the limited number of observations made at that time, we have undertaken to repeat the work, on water from a variety of different locations, and with certain improvements in the analytical method.

The details of the technique are described in the references in the earlier paper, but briefly it consists of boiling the dissolved gas out of the water sample under reduced pressure, adsorption on charcoal at the temperature of liquid air, and measurement of the non-adsorbable residue (helium and a constant fraction of the neon) by means of a McLeod gage. High vacuum technique is used throughout, and great care must be exercised in flushing out the line with pure electrolytic oxygen, removing traces of hydrogen by repeatedly passing over hot palladium.

Slight modifications in the original method consisted of increasing the size of the water sample to about 300 ml., an addition to the line to permit flushing the gas out of the boiling flask by means of oxygen, instead of depending entirely upon water vapor, and a graphic method of calculating results from the McLeod gage readings.

Because of the extremely small size of the gas sample measured (less than 10^{-5} ml.) a capillary of about 0.1 mm. diameter must be used in the McLeod gage. To eliminate the effect of capillary depression upon the mercury level a series of readings was taken for each measurement, at different pressures. When these are plotted graphically the slope obtained is a measure of the volume of gas trapped. This practice largely overcame the great variability in capillary depression which was observed from time to time. It was impossible to determine a constant factor for a given tube. Electrodeless discharge in the capillary, for the purpose of testing the residual gas for hydrogen, was found to change the glass surface so much as to make the tube practically useless.[4]

Water samples were collected in the routine manner at sea, by means of reversing water bottles, and stored in glass citrate bottles, completely filled, to prevent exposure to the air. A method of doing this has been described.[5] From these the water was introduced into the boiler by direct mercury displacement, with only momentary and non-turbulent exposure to the air, a major improvement over the earlier method of pouring from the storage bottle.

The oxygen determinations were made by the routine Winkler method, on shipboard, immediately after collecting the samples.

The results are given in Table I. The five stations chosen present a complete array of conditions, in regard to the oxygen minimum. Four are in the Atlantic and one in the Pacific, the latter being almost entirely depleted of oxygen at a depth of about 600 meters. One of the Atlantic stations, 3113, is in the Sargasso Sea, south of the Gulf Stream; two others somewhat to the north. The oxygen minimum at these three varies from 200 to 900 meters. The last station, 2822CG, shows no oxygen minimum whatever.

In none of these is there any consistent relation between the oxygen and the helium–neon content, nor indeed any regular variation in the latter. We can only conclude that the earlier results, based upon a few observations at only two stations, were in some way fortuitous.

We were also unable to notice any significant difference between the solubility of the helium–neon mixture in sea water at 6 and at 23°, or in normal sea water diluted to half its original salinity, the figures obtained in these three respective cases being 16.9, 16.4, and 17.6.

Although the results obtained from the water of the Pacific are higher than all the others, we do not think this represents a real difference. These determinations were made several months after the others, with a different McLeod capillary and a number of other conditions altered. Nevertheless, although they probably cannot be compared

---

[1] This work was made possible by a grant from the Elizabeth Thompson Science Fund.

[2] Present address: Department of Chemistry, University of Rochester.

[3] Urry, This Journal, **57**, 657 (1935).

[4] In the earlier work a spectroscopic examination was regularly made, by means of an electrodeless discharge in the capillary, after the measurements had been taken. This necessitated a frequent change of capillary.

[5] Rakestraw and Emmel, *Ind. Eng. Chem., Anal. Ed.*, **9**, 344 (1937).

TABLE I

	Depth, meters	Temp., °C.	Oxygen ml./l.	He-Ne ml./l. × 10^{-5}
Station 3025 35°-55′N 67°-39′W Apr. 7, 1938	0	18.28	5.15	18.5
	5	18.31	5.15	14.1
	25	17.97	5.05	15.2
	62	17.93	5.17	15.2
	166	17.92	5.15	15.2
	333	17.63	4.90	15.6
	622	15.62	4.10	15.9
	912	9.55	3.60	15.9
	1772	3.86	5.88	16.5
	2959	3.16	6.15	17.8
Station 3105 39°-20′N 70°-32′W July 14, 1938	0	...	4.92	13.5
	24	20.78		16.3
	47	17.78	4.80	15.9
	95	14.68	4.10	16.6
	189	14.27	4.58	17.4
	284	12.16	3.40	16.6
	378	9.10	3.21	15.4
	474	6.83	4.07	15.4
	568	5.41	4.78	15.6
	663	4.76		15.2
	717	4.47	5.59	15.9
	986	4.04	5.98	17.2
	1702	3.46	6.10	14.8
Station 3113 37°-01′N 74°-21′W Aug. 2, 1938	0	26.14	4.75	13.3
	21	25.81	4.76	13.1
	85	14.85	3.99	15.0
	171	9.18	3.14	14.3
	260	7.03	3.94	
	389	5.55	4.73	12.4
	435	4.88	5.25	13.9
	555	4.55	5.54	15.4
	722	4.19	5.84	
	1055	3.80	6.14	17.9
	1388	3.55	6.24	12.8
Station 2822CG 57°-25′N 48°-47′W July 26, 1938	95	3.54	6.64	15.4
	286	3.28	6.63	16.1
	531	3.22	6.67	15.0
	898	3.18	6.68	15.6
	1953	3.26	6.58	14.8
	3072	2.46	6.30	14.8
Pacific station 32°-34′N 117°-28′W Nov. 9, 1938	10	16.39	5.66	17.3
	25	14.67	5.93	20.5
	74	10.75	3.91	16.8
	199	8.83	2.11	16.9
	298	7.98	1.25	16.9
	503	6.11	0.32	16.8
	607	5.41	.26	18.9
	808	4.48	.48	16.8
	979	4.07	.49	17.3
	1121	3.69	.69	16.9

with those from the other stations, they clearly indicate a regular and consistent distribution at this particular station. This view is confirmed by the fact that at this stage two samples of sea water saturated with air at 23 and 24° showed helium–neon contents of 19.1 and 18.7, respectively, higher than the solubility measurements made earlier.

Occasionally, in the earlier part of this work, a determination yielded an impossibly low result, compared with a duplicate. This was sometimes the case even with water saturated with air. Although we never located the reason for this with complete certainty, it seemed to be connected with the process of letting the gas into the adsorption line from the boiling flask. After every movement at this point had been standardized, and especially after provision had been made for washing the gas into the line with excess oxygen, no trouble of this sort was experienced. It is possible that this was the cause of the two or three unusually low values in the previous investigation, leading to the assumption of a helium–neon minimum.

Summary

A repetition of earlier work, under more suitable and representative conditions, shows the sea to be practically saturated with helium and neon at all depths, with no evidence of any depth of minimum concentration, and hence no relation to the depth of oxygen minimum.

RECEIVED AUGUST 17, 1939

Contribution No. 229

TRANSPORT AND CONVERGENCE OF THE NORTH ATLANTIC DRIFT CURRENT COMPUTED FROM THE AVERAGE JANUARY PRESSURE DISTRIBUTION*

BY

EDWARD M. BROOKS

According to Montgomery (1936, 1938), one of the important effects of the wind blowing over the sea surface is its production of positive and negative convergence in the drift current, which is essentially limited to a surface homogeneous layer usually less than 50 meters thick. This convergence results from the net transport of the drift current at right angles to the wind, the magnitude of the transport being such that the deflecting force acting on it exactly compensates the wind stress. Of course, this involves the assumption that the drift current has come to equilibrium with the wind. To avoid boundary conditions, this theory should be applied only to the open ocean, away from coast lines and in deep water.

The purpose of this paper was to find the extreme variations of the transport and convergence of the drift current in the North Atlantic Ocean for average atmospheric conditions. Computations for January were carried out and compared with the results of Montgomery's investigation for July (Montgomery, 1936). Then the transport and convergence of the drift for the other months were estimated qualitatively from Defant's monthly average atmospheric pressure charts (Defant, 1917).

Two methods were employed in getting the January results. The first, following that used by Montgomery (1936), was based on gradient winds deduced from the January pressure distribution given by Defant (1917); whereas the second used direct wind observations collected by the Koninklijk Nederlandsch Meteorologisch Instituut (1919). As the first method has been adequately treated by Montgomery, only the second will be discussed here.

The wind speeds, which were estimated in Beaufort numbers, were converted into meters per second by use of the international Beaufort scale (Perlewitz, 1935). The formula used for getting the magnitude of the transport from the wind speed was

$$T = \frac{\tau_0}{f} = \frac{\rho\gamma^2 W_0^2}{2\Omega \sin L}$$

(Rossby and Montgomery, 1936), where T was the magnitude of the transport; τ_0, the shearing stress between wind and water; f, the Coriolis param-

---

* Contribution No. 229 of the Woods Hole Oceanographic Institution.

Reprint from SEARS FOUND. JOURN. MAR. RES.

eter; ρ, the density of the air; γ^2, a stress coefficient; W_0, the surface wind speed; Ω, the angular velocity of the earth's rotation; and L, the latitude. γ^2 was taken as 0.0025 to conform with the choice of $z_0 = 0.6$ cm., used in the computations from Defant's pressures.

The transport and convergence calculated by the wind observations method were on the average about 20% larger than those obtained by the pressure method. Although this difference might be more marked if it were not for the existence of some atmospheric stability tending to reduce the surface wind speed below its theoretical value for a homogeneous atmosphere, the order of magnitude of the discrepancy seems relatively insignificant in view of the uncertainty of the applicability of the theory behind either computation. A second difference of more interest is the greater irregularity of the transport vectors and convergence magnitudes obtained from the wind method. It is doubtful whether the irregularities in the average winds can be explained by such atmospheric features as fixed anticyclonic cells in the Azores "high" or a mean polar front at a certain distance off the American coast because the positions of such semi-permanent elements might be too variable. Both of the differences found must be largely due to the fact that Defant got pressure values by interpolation with smoothed isobars, whereas the Dutch institute tabulated all observations without regard for geographical continuity.

The January transport and convergence computed from the average pressures of Defant are presented in Table I and Figure 52. The resemblance of the January chart to the July chart is quite pronounced in regard to both the distribution of the transport vectors and the magnitudes of the convergence, largely due to the existence of prevailing westerly winds in the north portion and easterly trades in the south portion at both times of year. On the other hand, minor seasonal differences in drift current movement occur in connection with the difference in size and shape of the Azores "high," which is less circular and has a weaker central pressure in January than in July. The average January transport is generally larger than that of July, corresponding to greater strength of the Icelandic "low" and steeper pressure gradients in the trade-wind belt in January. Along the average high pressure belt convergence is smaller, and in the extreme south it is larger than in July. Also, negative convergence, or divergence, is more marked in the Newfoundland region in January, when the mean isobars have a definite cyclonic curvature.

Although Defant's monthly average pressure maps suggest that the January and July conditions stand at opposite extremes in the annual cycle of average pressure distribution, the changes from one month to the other are not strictly uniform, as indicated by the maps for intervening months. Consequently, the annual trend of the more important features of the drift current deserves analysis from the monthly maps, even though the total variations are small.

By use of the principle that the transport is directly correlated with the wind speed, and that the convergence is positive in an atmospheric "high" pressure area and negative in a "low," it is possible to discuss the annual variations which might be expected. In the trade-wind belt, the northward transport is largest in winter, but the maximum convergence comes in the early spring; while the minimum (though still large) transport and convergence occur in autumn, when the pressure gradient is weakest and the isobars have the least anticyclonic curvature. Along the ridge of the Azores "high," convergence is pronounced in May and again in December, when there is a secondary maximum. In the zone of the westerlies, the greatest transport (always toward the south) occurs in late autumn and in early winter, but the convergence is largest in the spring months, although even then divergence exists east of Newfoundland. The American coastal transport is most marked in the latter part of the winter, when the maximum

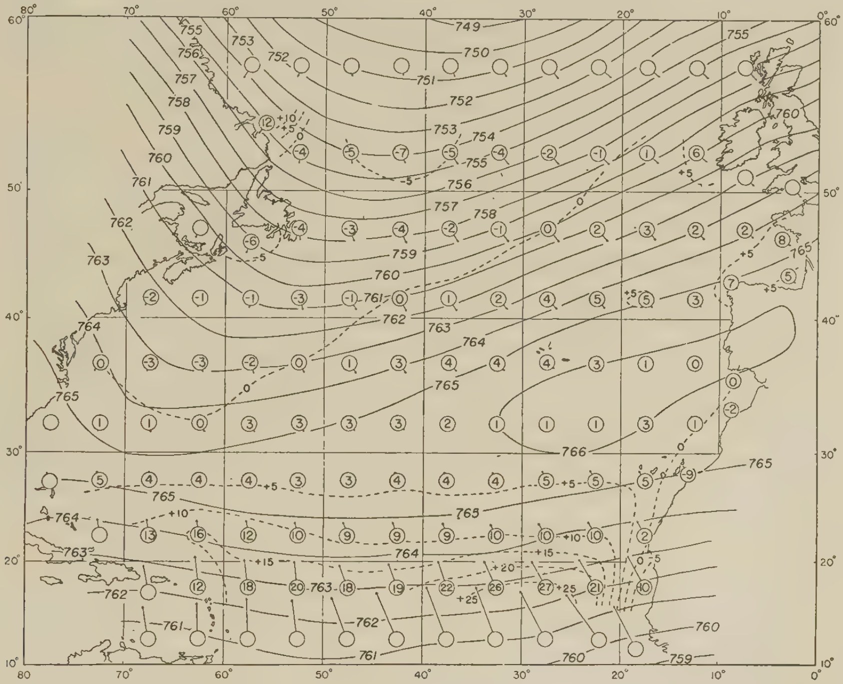

80° 70° 60° 50° 40° 30° 20° 10° 0°
60° 50° 40° 30° 20° 10°
749
750
751
752
753
754
755
756
757
758
759
760
761
762
763
764
765
766
755
756
757
758
759
760
761
762
763
764
765
760
759
+10 +5 0
-5
+5
+15
+20
+25
12 -4 -5 -7 -5 -4 -2 -1 0 6
-6 -4 -3 -4 -2 -1 0 2 3 2 2 8 5 7
-2 -1 -1 3 -1 0 1 2 4 5 5 3
0 -3 -3 -2 0 1 3 4 4 4 3 1 0 0
1 1 0 3 3 3 3 2 1 1 1 3 1 -2
5 4 4 4 3 3 4 4 4 5 5 5 9
13 16 12 10 9 9 9 10 10 10 2
12 18 20 18 19 22 26 27 21 40

Figure 52. The solid lines are average January isobars for each mm. Hg of atmospheric pressure. The vectors represent the transport of the drift current at the center of each 5° square. The figures in circles give the convergence of the drift current in cm./day. The dotted lines connect areas of equal convergence.

divergence occurs. There is little divergence in summer, when the trough of low pressure moves onto the continent. Along the African coast, divergence is most pronounced when the transport is directed as much off-shore as possible, which is the case in spring. In general, the magnitude of this divergence is directly correlated with the magnitude of the convergence in the trade-wind belt.

In conclusion, it might be stated that the characteristics of the average drift current were found to be more nearly constant during the year than might have been previously expected. However, it is obvious that, since a wind distribution and a corresponding atmospheric pressure field do not strictly match each other due to accelerations of the air, lateral atmospheric friction, and thermal stability, this sort of analysis could be improved by more accurate wind observations over a conveniently restricted area in the open ocean, for it is the actual wind rather than the pressure gradient which affects the drift current. To make best use of such wind observations, it would be necessary to apply a "smoothing" process similar to the smoothing of isobars, which process at the same time would not wipe out any real atmospheric discontinuities existing under average conditions. To test how closely the average is represented at any particular time, it might be advisable to compute the transport and convergence by days from a series of synoptic situations given on weather maps. The results of such a study might indicate, in addition to the average flow and convergence, possible temporary anomalies of the drift current configuration, which in some cases might appear in the form of incipient eddies with vertical axes.

REFERENCES

1. DEFANT, A.
1917. Luftdruckverteilung über dem nordatlantischen Ozean. Denkschriften der Kaiserliche Akademie der Wissenschaften, Vol. 93, p. 447.

2. KONINKLIJK NEDERLANDSCH METEOROLOGISCH INSTITUUT
1919. Publ. No. 110, Oceanographische en Meteorologische Waarnemingen in den Atlantischen Oceaan, Vol. for Dec., Jan., Feb. (1870–1914).

3. MONTGOMERY, R. B.
1936. Computation of the Transport of Surface Water due to the Wind System over the North Atlantic. Transactions of the American Geophysical Union, Seventeenth Annual Meeting, pp. 225–229.

4. MONTGOMERY, R. B.
1938. Circulation in Upper Layers of Southern North Atlantic Deduced with Use of Isentropic Analysis. Papers in Physical Oceanography and Meteorology, Vol. 6, No. 2, 55 pp.

5. PERLEWITZ, P.
1936. The Wind According to the Beaufort Scale and its Velocity. Hydrographic Review, Vol. 13, Part 1, p. 145.

6. ROSSBY, C.-G., AND MONTGOMERY, R. B.
1936. On The Momentum Transfer at the Sea Surface. Papers in Physical Oceanography and Meteorology, Vol. 4, No. 3, 30 pp.

TABLE I

Magnitude (tons/meter/sec) and Direction (Clockwise from N) of the Transport of the Drift Current for January

	80° W.		70° W.		60° W.		50° W.		40° W.		30° W.		20° W.		10° W.		0°		10° E.
60° N.					0.58 212°	0.34 197°	0.21 177°	0.21 169°	0.29 159°	0.37 148°	0.56 141°	0.67 131°	0.61 130°	0.62 132°	0.62 139°	0.53 141°	0.47 129°	0.25 124°	
					0.43 214°	0.33 192°	0.35 175°	0.38 158°	0.50 148°	0.56 143°	0.61 139°	0.63 136°	0.57 134°	0.48 131°	0.39 135°	0.37 140°	0.43 140°	0.44 —	
50° N.		0.11 —	0.16 221°	0.26 209°	0.37 204°	0.32 179°	0.44 162°	0.58 155°	0.60 145°	0.65 141°	0.64 139°	0.57 138°	0.45 139°	0.35 138°	0.25 133°	0.16 130°	0.10 119°		
		0.19 218°	0.11 218°	0.08 195°	0.19 194°	0.34 162°	0.44 151°	0.50 151°	0.50 145°	0.49 139°	0.45 138°	0.34 140°	0.22 146°	0.14 145°	0.11 140°	0.09 138°			
40° N.	0.08 217°	0.16 224°	0.14 202°	0.17 167°	0.27 161°	0.31 153°	0.34 146°	0.36 146°	0.31 139°	0.22 138°	0.12 135°	0.07 145°	— —	— —	— —				
	0.03 228°	0.09 199°	0.15 180°	0.21 153°	0.23 152°	0.20 151°	0.13 144°	0.07 137°	0.04 129°	— —	— —	— —	0.04 305°	0.05 307°	0.04 317°				
30° N.	0.14 341°	0.08 350°	0.03 351°	— —	— —	— —	— —	0.03 343°	0.08 340°	0.12 333°	0.22 337°	0.31 331°	0.33 331°	0.23 330°					
	0.70 —	0.65 351°	0.61 352°	0.53 354°	0.57 352°	0.48 347°	0.48 342°	0.52 340°	0.45 339°	0.43 332°	0.52 327°	0.58 332°	0.65 331°						
20° N.		1.44 —	1.52 349°	1.72 354°	1.52 352°	1.35 352°	1.21 341°	1.28 339°	1.46 341°	1.57 336°	1.65 331°	1.83 330°	2.03 331°						
			1.84 350°	2.06 359°	2.42 358°	2.37 352°	2.66 340°	3.15 337°	3.48 339°	3.49 339°	3.43 332°	3.50 323°	2.99 332°						
10° N.																			

Contribution No. 230

CONSIDERATION OF THE DEPTH OF THE MOTIONLESS SURFACE NEAR THE GRAND BANKS OF NEWFOUNDLAND

By

FLOYD M. SOULE

U. S. Coast Guard and
*Woods Hole Oceanographic Institution**

In physical oceanography the admitted limitations of the Bjerknes circulation theorem sometimes are lost sight of and therefore the current trend of inquiring emphasis on these limitations is encouraging. The intelligent interpretation of dynamic calculations and the determination of absolute current directions and velocities therefrom, depend upon a knowledge of the location and shape of a motionless reference surface. In the past the arbitrary selection of isobaric surfaces for reference has been the resort to an approximation found useful in the absence of more definite knowledge regarding the true location and shape of such a motionless surface or surfaces. In recent years various oceanographers have proposed various non-spheroidal reference surfaces such as the oxygen-minimum layer, and a surface approximating an isentrope of constant vertical stability. The state of our knowledge has not yet reached the point where we can define such a surface which is universally applicable. Until that stage of development is reached each unique region must be dealt with individually and the several particular solutions may help in ultimately laying bare that general solution.

In the southern part of the Labrador Sea the oxygen minimum surface cannot be used since it is not present. Observation and experience of the International Ice Patrol has shown that the direction and velocity of the surface currents as indicated by the drift of icebergs are essentially in agree-

---

* Contribution No. 230.

Reprint from SEARS FOUND. JOURN. MAR. RES.

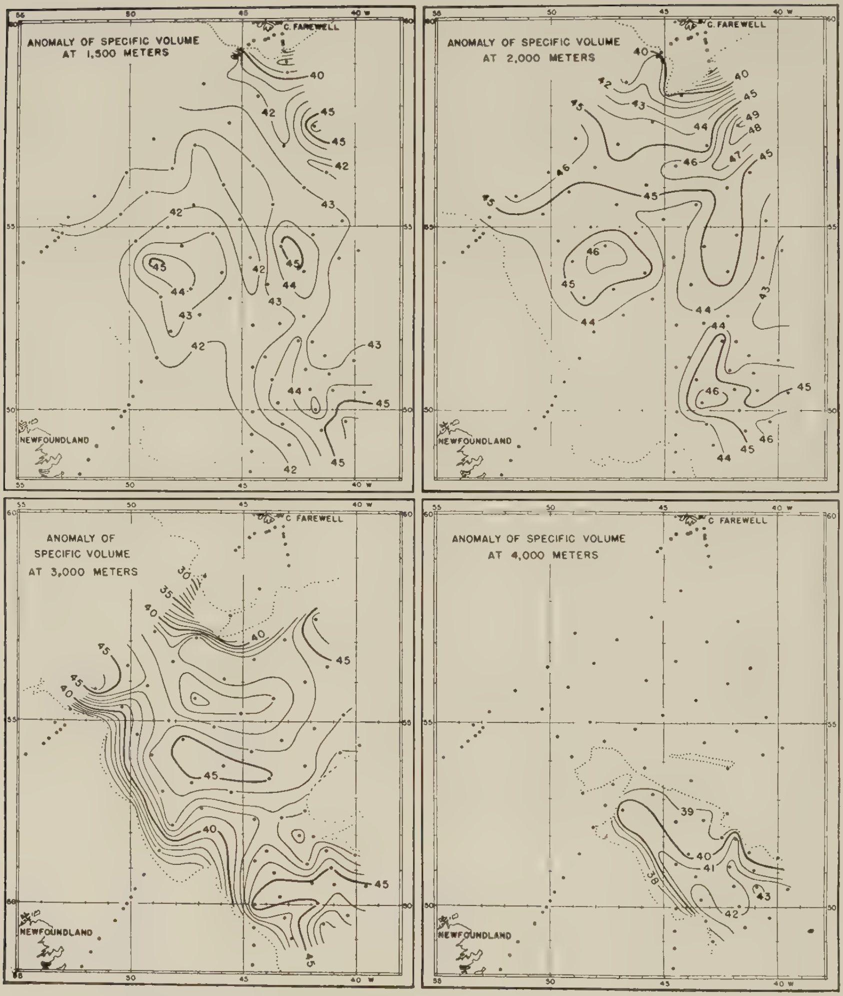

ANOMALY OF SPECIFIC VOLUME AT 1,500 METERS
ANOMALY OF SPECIFIC VOLUME AT 2,000 METERS
ANOMALY OF SPECIFIC VOLUME AT 3,000 METERS
ANOMALY OF SPECIFIC VOLUME AT 4,000 METERS
C. FAREWELL
NEWFOUNDLAND
55
50
45
40 W
60

Figure 53. Horizontal distribution of anomaly of specific volume.

ment with dynamic topographic maps referred to the 1500-decibar surface. Prior to 1935 deeper reference surfaces were not used for this region chiefly because of the errors which would have been introduced through necessary extrapolations in the many cases where observations did not extend to deeper levels. However, during the summer of 1935 a network of stations in this area were all occupied to as near bottom as was practicable and the question arose as to what reference surface would be the best.

In order to find the most nearly motionless level in the area as a whole the least variability in vertical differences in dynamic height for any 500-meter layer was selected as a criterion. The investigation showed that the desired level was at about 2000 meters. The method was then checked by inspection of horizontal gradients of anomaly of specific volume. Figure 53 shows the horizontal distribution of anomaly of specific volume for the 1500-, 2000-, 3000-, and 4000-decibar surfaces and demonstrates that the horizontal gradients are least in the 1500- and 2000-decibar surfaces. It will also be seen that with the exception of the region immediately south of Cape Farewell, the 2000-decibar surface is indicated as most nearly motionless on the basis of this criterion. Such a criterion rests on an assumption which at that time was reasonable but without proof. Restated, the assumption was that the surface in which the velocity was most nearly uniform was also the surface in which the velocity was most nearly zero.

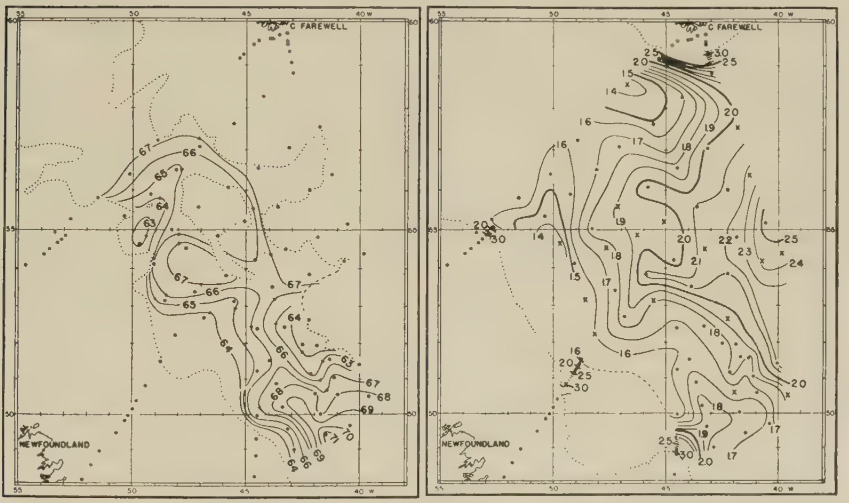

55
50
45
40 W
60
55
50
C FAREWELL
NEWFOUNDLAND
67
66
65
64
63
67
66
65
64
67
64
66
63
67
68
69
68
70
69
66
64
55
50
45
40 W
60
55
50
C FAREWELL
NEWFOUNDLAND
25
30
20
25
15
14
20
16
19
17
18
16
20
30
14
19
20
22
25
23
24
18
21
15
17
18
16
16
20
25
30
20
18
17
25
19
30
20
17

Figure 54. At left: Dynamic topography at 3,500 decibars relative to 2,000 decibars. At right: Potential bottom temperatures.

Deep level dynamic topographic charts were then drawn with reference to the 2000-decibar surface and these gave a circulation picture of the deep water consistent with other criteria of the circulation of the deep and bottom waters of the Labrador Sea. Admittedly, because of the small density gradients involved and because of the probably undulatory character of the motionless surface if one exists, the accuracy of deep level current maps is highly questionable as to velocity. It is believed, however, that the indicated directions of flow are reliable in the main. One bit of evidence confirming these maps, and therefore the selection of the motionless surface, is to be found in examining the bottom temperatures. From the material of this survey it was possible to construct a reliable chart of the potential temperature at bottom. Figure 54 shows the dynamic topographic map of the 3500-decibar surface relative to 2000 decibars and the potential bottom temperatures for depths greater than 1500 meters. Each part of this figure will be seen to indicate the southward movement of water along the American side of the basin.

During the summer of 1937 an adjacent area to the south, east of the Grand Banks, was surveyed. At many of the stations the observations extended to 4000 meters. Although these stations were so widely spaced that it is not possible to deduce from them detailed patterns of circulation, they nevertheless afforded the opportunity of studying the major features. In a manner similar to that used in the 1935 survey, the horizontal distribution of anomaly of specific volume was examined by means of the construction of horizontal sections for several of the deeper levels. Inspection of these sections indicated that the smallest horizontal gradients of anomaly of specific volume occurred at 2000 or 2500 meters depth. Again using this as the criterion of least motion, the 2000-decibar surface was selected for reference in the construction of dynamic topographic maps. In Figure 55 is shown the resulting topography at the surface of the sea and at 3500 decibars both referred to the 2000-decibar surface. The picture of the circulation at the sea surface is in accord with the direction of drift indicated by the wire angle at stations where light wind or calm weather prevailed, and with the set indicated by astronomical observations on runs between stations. Further verification is found in the depth of the 10° isotherm. Iselin (*1*) has found this to be a convenient indicator of the circulation in the western North Atlantic and examination of those stations taken in or near the Atlantic Current shows a notable correspondence between the contour lines of this thermal surface and the indicated course of the dynamic isobaths.

Examination of the anomalies of dynamic height at levels below 2000 decibars with reference to that surface indicated increasing relative velocities to 3500 decibars and a decrease from 3500 to 4000 decibars. In the preceding discussion of the 1935 survey of the adjacent area to the north it was pointed out that the deep water was moving southward along the American side. Here we see the continuation of this southward flow of the deep water past Flemish Cap and continuing as far as latitude 40° N., the southern limit of the survey. Most of the flow continues close in to the edge of the Grand Banks but some of it travels more directly southward along the 41st meridian, being separated from the major portion by a whorl which is roughly concentric with the bottom depression at about 44° N., 42° W.

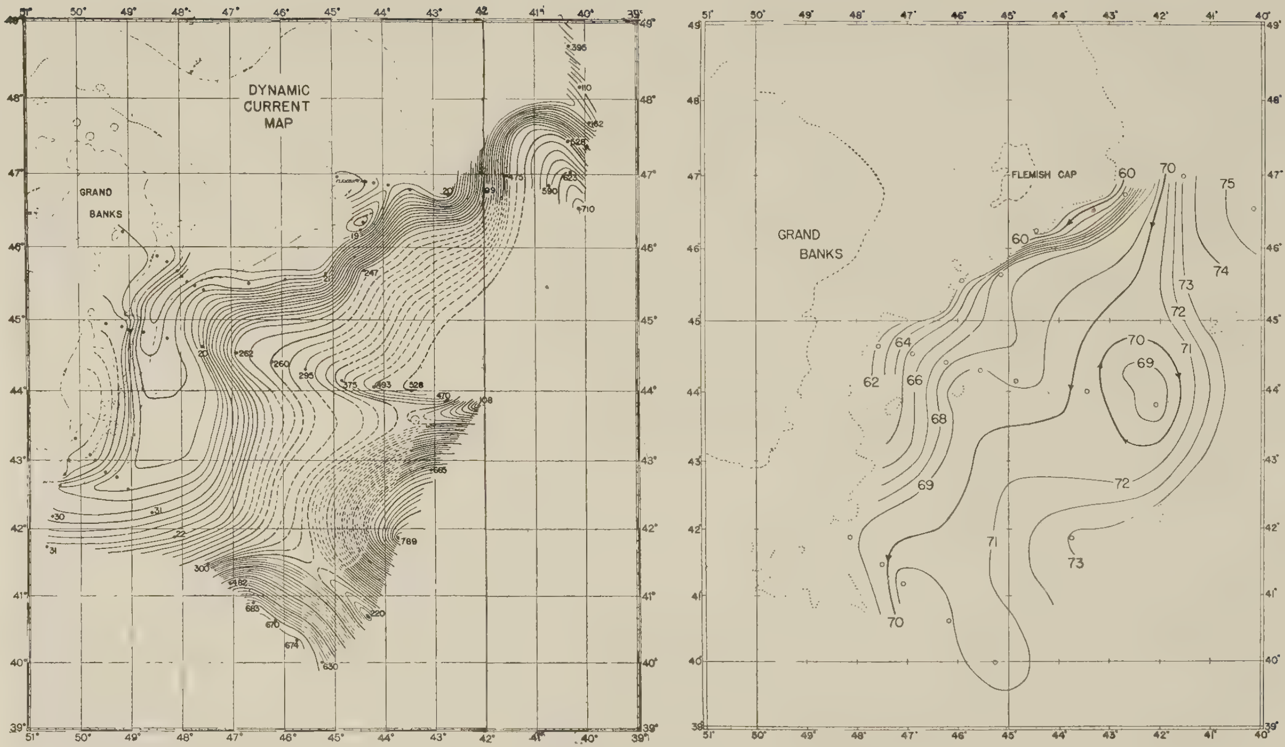

DYNAMIC CURRENT MAP
GRAND BANKS
GRAND BANKS
FLEMISH CAP
60
70
75
74
73
72
71
70
69
64
62
66
68
69
72
71
73
70

Figure 55. Dynamic topography at the surface and at 3,500 decibars, both referred to 2,000 decibars.

Now a rough check on the assumption that the 2000-decibar surface is most nearly motionless is made possible by the distribution of the isobaths in the 3500-decibar map with respect to the overlying Atlantic Current. The volume of flow of the Atlantic Current past the section east of Flemish Cap, determined by numerical computation and checked by planimeter measurements of a velocity profile, was 39.3 million cubic meters per second relative to the 2000-decibar surface. At 3500 decibars the velocity is greater at this section than in any other part of the survey. If the 2000-decibar surface is motionless the average velocity in this section at the 3500-decibar surface is 6.6 centimeters per second southerly and the average velocity of the water in the rectangular cross section between the 2000- and 3500-decibar levels is taken at 3.3 centimeters per second southerly. However, if the 3500-decibar surface is motionless the average velocity is 6.6 centimeters per second northerly at 2000 decibars; the average velocity in the rectangle is 3.3 centimeters per second northerly; and all of the velocities used in determining the volume of flow of the Atlantic Current above 2000 decibars are too small by 6.6 centimeters per second in which case the volume of flow of the Atlantic Current past this section becomes 39.3 + 25.5 + 9.7 or 74.5 million cubic meters per second northerly.

Now the 3500-decibar map indicates that the deep water velocity past the section running southeasterly from the Tail of the Grand Banks is much less than it is east of Flemish Cap. Again taking the 2000-decibar surface as motionless, the average velocity at the 3500-decibar surface at the southern section is 2.6 centimeters per second southerly, whereas if the 3500-decibar surface is motionless this represents the average northerly velocity at 2000 decibars. If half this figure or 1.3 centimeters per second be taken as the average velocity of the water between the 2000- and 3500-decibar surfaces under the Atlantic Current at this section, the resulting volume of flow between these surfaces is about 5.9 million cubic meters per second, directed northerly if 3500 decibars is the motionless surface and directed southerly if 2000 decibars is the motionless surface. Furthermore, if the 3500-decibar surface is motionless any determination of the volume of flow above 2000 decibars relative to that surface will be based on velocities which are uniformly too low by 2.6 centimeters per second which will result in a discrepancy of 15.8 million cubic meters per second. Thus if the 3500-decibar surface is motionless, and we assume that the Atlantic Current passing the Flemish Cap section is the same as the Atlantic Current passing the southern section, a determination of the volume of flow past the latter section from 0 to 2000 decibars relative to 2000 decibars should give 74.5 − 5.9 − 15.8, or 52.8 million cubic meters per second; but if the 2000-decibar surface is motionless, the result should be 39.3 million cubic meters per second. Numerical computation, again checked by planimeter measurements of a velocity profile of the Atlantic Current past this southern section, actually showed a volume of flow of 42.8 million cubic meters per second, which is much nearer the figure of 39.3 than the alternate figure of 52.8. Restating these figures in another manner: if the 3500-decibar surface was motionless the Atlantic Current in passing from the southern section to the Flemish Cap section increased from 64.5 to 74.5 or 10 million cubic meters per second which is 15½%, whereas if the 2000-decibar surface was motionless the Atlantic Current decreased from 42.8 to 39.3 or 3.5 million cubic meters per second which is 8%. Considering that we have been discussing only the northern branch of the Atlantic Current and considering the assumption that the volume of flow past the two sections is the same, the foregoing would seem to indicate that the 2000-decibar surface is more nearly motionless than the 3500-decibar surface.

Attention is again directed to the other assumptions made in this transport balance; namely, that the deep water velocities are sufficiently reliable to make the check significant, and that the vertical distribution of the deep water velocity is near enough to being linear for the purpose of the check.

From the dynamic topographic maps of the sea surface and the 3500-decibar surface, as well as other maps not shown, the direction of flow is indicated to have been roughly parallel to the bottom contours at all levels. This is true regardless of the reference surface selected, only the direction of flow along the dynamic isobaths being dependent upon the selection of the proper reference surface. In other words at any level the flow is either from the Tail of the Grand Banks toward Flemish Cap or from Flemish Cap toward the Tail of the Grand Banks. The temperature-salinity correlation was investigated at each end of the area surveyed. All of the observations from depths greater than 1500 meters from the stations comprising the section east of Flemish Cap were plotted and the individual station curves drawn. These are shown at the left in Figure 56. The two broken lines, separated by about 0.03 °/₀₀ salinity, represent approximately the range of observational error. A similar plot of temperature against salinity was made for all observations from depths greater than 1500 meters from the stations comprising the section running southeasterly from the Tail of the Grand Banks and is shown in the middle of Figure 56. Again the individual station curves have been drawn and the envelopes indicated by broken lines. The separation of the envelopes is again about the range of observational error except in the vicinity of about 3.25°, where the characteristic shape of the individual station curves require a lower-salinity hump. From these two plots have been derived the mean curves representing the temperature-salinity correlation for the two extreme edges of the survey, along the course of the current, for depths greater than 1500 meters, and shown at the right in Figure 56. From this it will be seen that the two correlation curves cross and that in the upper part of the figure the water off Flemish Cap is fresher than off the Tail of the Banks, whereas in the lower part of the plot, in the deeper water, that off the Tail of the Banks is fresher than that off Flemish Cap. Now if we consider that the source of this fresher water of more negative salinity anomaly is the downward-mixing, cabbeling (*5*), mixed water containing Labrador Current water as a constituent and found along the boundary between the Labrador and Atlantic Currents (*3*) (*4*), then the interpretation is that in the upper levels the Atlantic Current is traveling from the Tail of the Banks toward Flemish Cap, which we know to be the case, and that in the deeper levels the water below the Atlantic Current is moving in the opposite direction, from Flemish Cap toward the Tail of the Grand Banks. The corollary is that at some level in between, the water is motionless and that this motionless level is at about where the two curves shown at the right in Figure 56 cross. The presence of the hump in the curve for the Tail of the Grand Banks makes it difficult to say from this figure where this motionless level is located more exactly than that it is between temperatures of about 2.7° and 3.4° C. which correspond to depths of about 3200 and 1750 meters respectively. This is looked upon as strong evidence in favor of the existence of a motionless surface such as was assumed in the construction of the dynamic topographic maps referred to the 2000-decibar surface, the depth of which surface is within the limits indicated from this consideration of the temperature-salinity correlations.

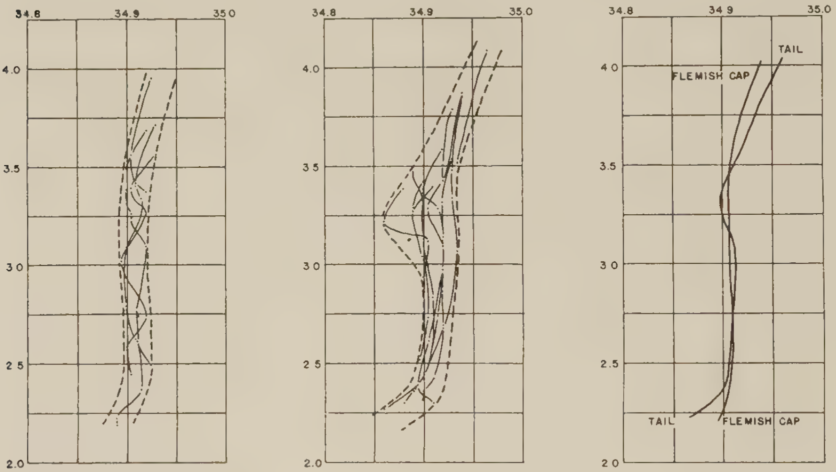


Figure 56. Temperature-salinity correlation for depths greater than 1,500 meters. Left: Stations 2523–2528 occupied July 7–9, 1937, east of Flemish Cap. Middle: Stations 2475–2484 occupied June 22–25, 1937, southeast of the tail of the Grand Banks. Right: Comparison of mean curves.

Because it was indicated, on the assumption of the 2000-decibar surface as the most nearly motionless, that the most rapid motion of the deep water occurs in the 3500-decibar surface, this surface was selected for the illustrations which have been described. For the same reason and for comparison with the dynamic topography of the 3500-decibar surface referred to the 2000-decibar surface a potential density surface of $\sigma_{t_\varphi} = 27.90$ was selected for an isentropic (*2*) analysis since the depth of this density surface is in the neighborhood of 3500 meters. Potential temperatures at this isentropic surface have been determined and isotherms have been drawn for the same survey from which was derived the deep level current map which has figured in the foregoing discussion. For purposes of comparison, Figure 57 shows this dynamic topographic chart of the 3500-decibar surface relative to 2000 decibars at the left, and the isothermal chart of potential temperature at the surface of $\sigma_{t_\varphi} = 27.90$ at the right. The axis of minimum temperature is the most striking feature of this illustration and has been traced in as a heavy broken line. It indicates the flow of the cold deep water from the Labrador Sea southward beneath the Atlantic Current. This is the same general picture of the circulation of the deep water that is given by the topographic chart at the left. The similarity of the two parts of the illustration is considered to be a further confirmation of the approximation to zero velocity at the 2000-decibar surface since this is the reference surface used in the construction of the dynamic topographic map shown. As was pointed out earlier in connection with the topographic map the stations are so far apart that details of circulation cannot be derived from the map. This is of course also true for the isothermal chart of the isentropic surface shown. All of the isotherms might well be drawn as broken lines to indicate the uncertainty as to their course. However, this much is regarded as certain: that the axis of minimum potential temperature is well defined and the southward flow clearly indicated. There is a choice open as to whether the axis passes east or west of the central station at the north end of the diagram. In the isentropic analysis the axis has been shown as passing east of this central station in order to preserve the simplest diagram. In the dynamic chart the axis seems to pass to the west of this central station. The main point is that the two circulation pictures are in general agreement.

Perhaps it should be emphasized here that the idea of flow along an isentropic surface is subject to the same necessity for proof that confronts the Bjerknes circulation theorem. It is subject to limitations and a very pertinent limitation in the region under discussion is that the flow is not isentropic in regions where cabbeling is taking place. It has already been mentioned that along the boundary of the Labrador Current cabbeling is in evidence. The left hand edge of this isentropic chart is therefore questionable. This presence of cabbeling may be a factor in the reason for the

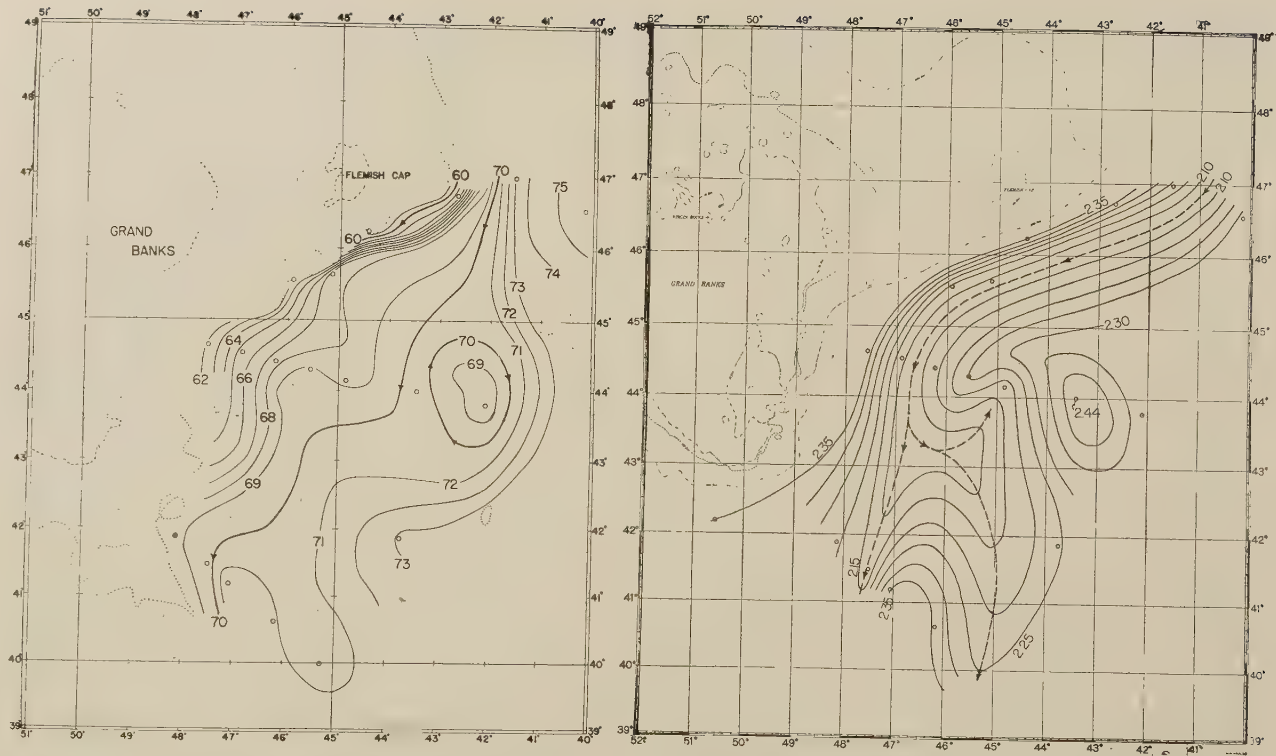

FLEMISH CAP
GRAND BANKS
60
70
75
74
73
72
71
70
69
64
62
66
68
69
72
71
73
70
210
210
235
230
244
235
215
235
225
GRAND BANKS

Figure 57. Left: Dynamic topography at 3,500 decibars relative to 2,000 decibars. Right: Potential temperature at isentropic surface of $\sigma_{t_\varphi} = 27.90$.

variable depth of the isentropic surface selected. Figure 58 illustrates the extent of this variation in depth. Here the depth of the isentropic surface has been plotted for each of three sections across the axis of minimum potential temperature. In each case the western end of the section is at the left. The broken vertical lines indicate the intersection of the cold axis with the various sections. The three curves have been so oriented that the intersections with what is regarded as the major cold axis have a common abscissa. This illustration shows that in each of the sections the depth of the surface shoals abruptly in approaching the western end. This is noted because it is particularly along the western edge of the figure that cabbeling probably occurs. The figure also illustrates the degree to which the depth of the isentropic surface approaches that of the 3500-decibar surface.

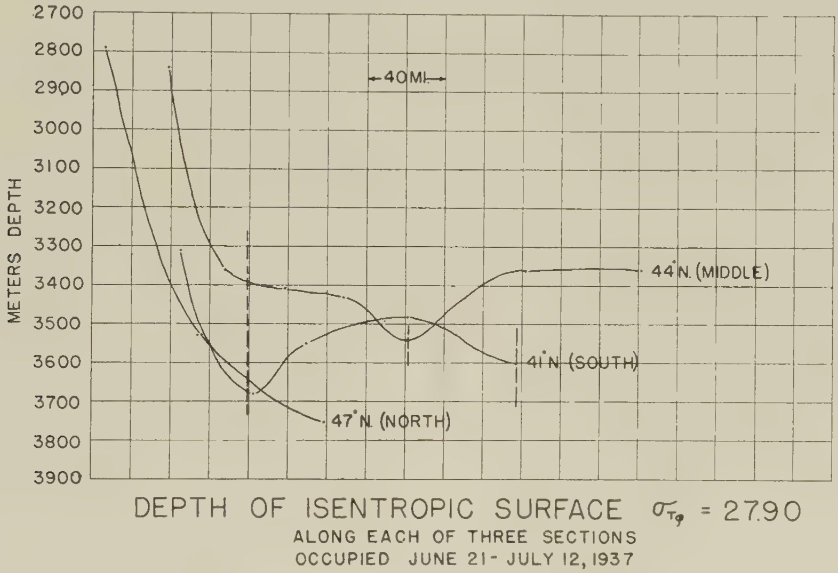


Figure 58. Three profiles through isentropic surface of $\sigma_{t_\varphi} = 27.90$.

We have now considered a number of indicators all of which are in substantial agreement in support of the existence of a most nearly motionless level at a depth of about 2000 or 2500 meters in the region immediately eastward of the Grand Banks. Summarizing, this evidence is contributed by patterns of flow, bottom temperatures, a volume transport balance, temperature-salinity correlations, and a deep-water isentropic analysis.

References

(*1*) Iselin, C. O'D.

1936. A study of the circulation of the Western North Atlantic. Papers in Phys. Oceanog. and Met. M. I. T. and W. H. O. I., pp. 69–72, Vol. IV, No. 4, Cambridge, Mass.

(*2*) Montgomery, R. B.

1938. Circulation in upper layers of southern North Atlantic deduced with use of isentropic analysis. Papers in Phys. Oceanography and Met. M. I. T. and W. H. O. I., pp. 11–14, Vol. VI, No. 2, Cambridge, Mass.

(*3*) Smith, Edward H., Floyd M. Soule and Olav Mosby

1937. The *Marion* and *General Greene* expeditions to Davis Strait and Labrador Sea. Scientific results, physical oceanography. pp. 137 and 175–179, U. S. Coast Guard Bull. No. 19, part 2. Washington.

(*4*) Soule, Floyd M.

1938. International Ice Observation and Ice Patrol Service in the North Atlantic Ocean—Season of 1936. Oceanography, p. 51, U. S. Coast Guard Bull. No. 26. Washington.

(*5*) Witte, Emil

1910. Aspiration infolge der Mischung von Wasser. Geographischer Anzeiger. Oktober.

Contribution No. 232

PLANKTON STUDIES. II. THE WESTERN NORTH ATLANTIC, MAY-JUNE, 1939*

By

GORDON A. RILEY

Bingham Oceanographic Laboratory, Yale University

The results of the first paper of this series, a study of the plankton in a tropical shallow water region in the Gulf of Mexico, suggested the desirability of extending the observations to more typically oceanic areas in order to analyze productivity factors in relation to the depth of water and to attempt to estimate the relative productivity of northern and southern seas. Opportunity for such an investigation was obtained during a cruise of the "Atlantis" from the northern coast of Cuba to Woods Hole. Eighteen stations were established during the cruise, and measurements were made at each station of temperature, oxygen, phosphate, nitrate, and total plant pigments from the surface to the approximate limit of the occurrence of phytoplankton. In the surface waters of all stations the chlorophyll content was also determined, and experimental measurements were made of the oxygen and nitrate production and consumption in light and dark bottles. Finally, at five of the stations, quantitative collections of zooplankton were made with Clarke plankton samplers.

I am greatly indebted to the Woods Hole Oceanographic Institution for providing me with the facilities for this work. I should like also to thank Mr. Albert E. Parr and Mr. G. Evelyn Hutchinson for examining and criticizing the manuscript, Dr. George L. Clarke for providing me with plankton samplers, and Mr. Alfred Woodcock, Dr. Henry Mahncke, and Mr. Dean F. Bumpus for help in the collection of materials.

METHODS

The methods used for the determination of total plant pigments, chlorophyll, and oxygen were the same as in the first paper of this series. Nitrates were measured by means of the diphenylbenzidine method of Atkins (1932). In testing this method it was found that analytical errors could be reduced by doubling the quantity of sea water and reagents used in order to minimize the error involved in measuring out small volumes of fluid. Otherwise the method used was exactly as described by Atkins.

---

* Joint contribution from Woods Hole Oceanographic Institution (No. 232) and Bingham Oceanographic Foundation.

Reprint from SEARS FOUND. JOURN. MAR. RES.

Work by Cooper (1938) on the salt error in determinations of phosphate makes it necessary to specify the exact conditions of the test. The original Atkins-Deniges method was used, with 2 ml. of molybdate reagent per 100 ml. of water, and the comparison was made in a Bausch and Lomb colorimeter with 100 mm. cups. The salt error unfortunately was not determined for each analysis, but measurements made later on three samples of surface water collected during the cruise gave an average of 1.39. Since this is somewhat higher than the usual values, and moreover since the reagents were contaminated (an amount equivalent in the ordinary conditions of the test to a concentration of about 0.15 mg. atoms of P per m^3 in sea water), which magnified the error in the determination of small quantities of phosphate, the values given should be regarded only as approximate.

The experiments were conducted in the following way: 250 ml. bottles were filled with surface water in the same manner as for routine oxygen tests. The bottles were exposed for a period of three days. When the vessel was in port, the bottles were hung over the side at a depth of one meter in a position where they would receive direct sunlight all day. This included the first three stations and parts of six others. At sea it was necessary to adopt a makeshift procedure in which the bottles were suspended in a tub on deck, and the water in the tub, surrounding the bottles, was changed frequently in order to maintain a normal temperature. Duplicate experiments performed during the early part of the cruise showed no significant difference in the results of the two methods. At the end of the period of exposure, the bottles were shaken thoroughly before being unstoppered. One milliliter of water was then removed for a nitrate test, and the Winkler reagents were immediately added to the remainder.

LOCATION OF STATIONS

The positions of the stations are shown in Figure 49. Eight of the Stations, 3491 to 3512 inclusive and 3523, were in the Gulf stream. Five of them, 3513 to 3520, were in the Sargasso Sea. All these, and in addition Station 3486, off the coast of Cuba to the east of the Florida Straits, may be regarded as tropical waters, in the sense that they were in regions of high and relatively constant temperature, although the conditions were different from what is found in equatorial waters. The three northernmost stations were typical North Atlantic slope waters, and the remaining one, 3528, apparently was transitional, but was more nearly characteristic of northern than of tropical water.

TEMPERATURE AND LIGHT

The surface temperature in the southern areas varied from 22° to 27°, the higher temperatures being found in the Gulf Stream and the Florida

Straits and the lower ones in the Sargasso Sea. In the latter there was a decrease of three or four degrees in the first hundred meters and little further change in the next three hundred. In the Gulf Stream, on the other hand, there was a fairly distinct thermocline lying somewhere between one hundred and three hundred meters below the surface.

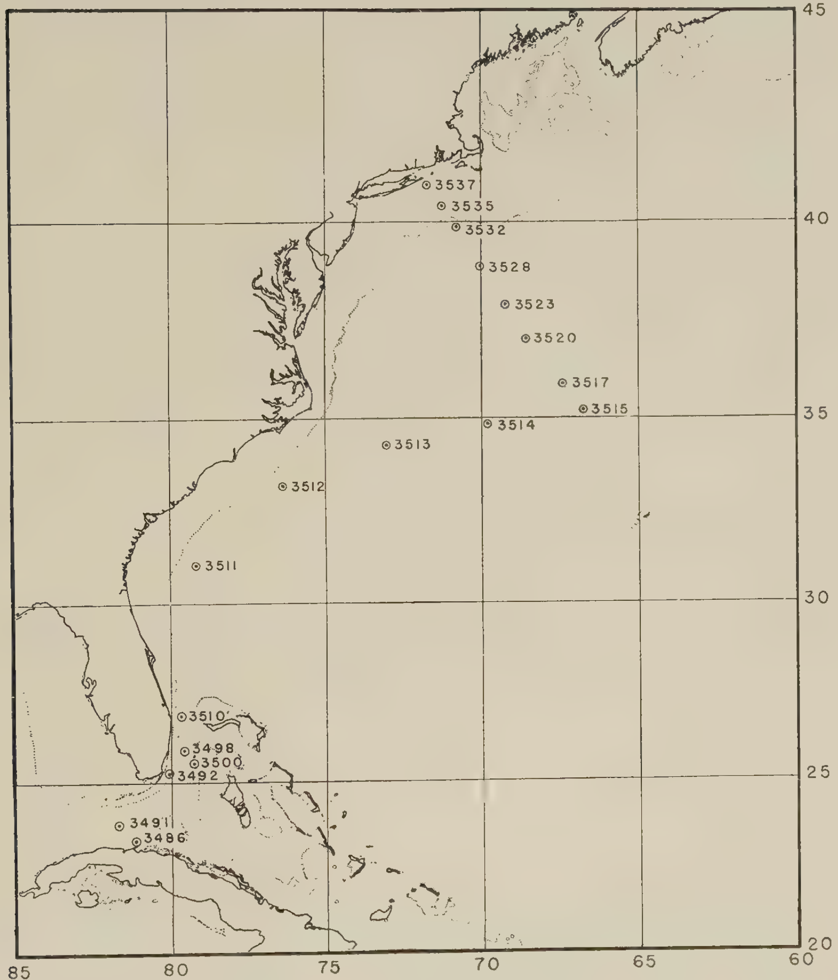

45
40
35
30
25
20
85
80
75
70
65
60
3537
3535
3532
3528
3523
3520
3517
3515
3514
3513
3512
3511
3510
3498
3500
3492
3491
3486

Figure 49. Station numbers and positions.

At the three northernmost stations, the surface temperature was from 10.63° to 12.52°, and at Station 3528, designated above as transitional, it was 19.67°. The thermocline probably lay at about 25 m. throughout most of this area.

The normal radiation for the region studied was estimated roughly by interpolation of data given by Kimball (1928). The normal total radiation is approximately the same for the entire region during May and early June, the greater light intensity in the south being compensated by the longer day in the north, and the total estimated range being from 456 to 462 g. cal. per cm^2 per day. Therefore, in comparing plankton conditions at different latitudes it is unlikely that variations can be ascribed to differences in radiation, unless the season was quite abnormal.

THE STANDING CROP OF PHYTOPLANKTON

The collection of materials for analyses of plant pigments and chlorophyll was made by filtering two or three liters of water through a Whatman No. 2 filter paper. No analyses were made of net plankton.

The analyses of surface phytoplankton in the southern waters, summarized in Table I, are slightly higher but of the same order of magnitude as the shallow water determinations reported in the previous paper (average 1300 Harvey units per m^3 in the present work, and in the Tortugas region 924 units). The mean of the five stations in the very deep water of the Sargasso Sea is slightly less, 860 units.

TABLE I

Plant Pigments and Chlorophyll in the Surface Waters

	Tropical Waters (14 analyses)	*Northern Waters (4 analyses)*	*All Analyses*
Plant pigments (Harvey units per m^3)			
Maximum	3500	8300	8300
Minimum	600	1700	600
Mean	1300	4100	1900
Chlorophyll (Mgs. per m^3)			
Maximum	2.5	3.6	3.6
Minimum	0.4	1.4	0.4
Mean	1.0	2.1	1.2

The maximum quantity of phytoplankton probably occurs somewhere between the surface and 100 m. In all but two of the analyses of tropical waters, the quantity of plant pigments was greater at 100 m. than at the surface. The maximum depth of occurrence is sometimes 400 m. or more, three out of five analyses at that depth yielding slight but detectable quantities of plant pigments.

The four analyses of northern surface waters yielded a mean of 4100 Harvey units of pigments per m³ and 2.1 mgs. of chlorophyll. The plant pigments were three times as high as in the southern waters, and the chlorophyll was twice as high. The vertical distribution of plant pigments at the two northern deep water stations is shown in Figure 50, together with the mean distribution in all the southern waters examined. It is evident from the figure that not only is the northern phytoplankton concentrated in a much shallower stratum of water, but also that the total quantity of plant pigments is considerably greater in the south. The plant pigments per unit area were determined roughly by interpolation between successive levels, with the following results: mean of the four analyses of northern waters—143,000 Harvey units per m²; mean of the two northern deep water stations—197,000 units; mean of the fourteen southern stations—345,000 units. Even the most completely oceanic stations, the five analyses in the Sargasso Sea, showed a larger standing crop than the northern stations, the

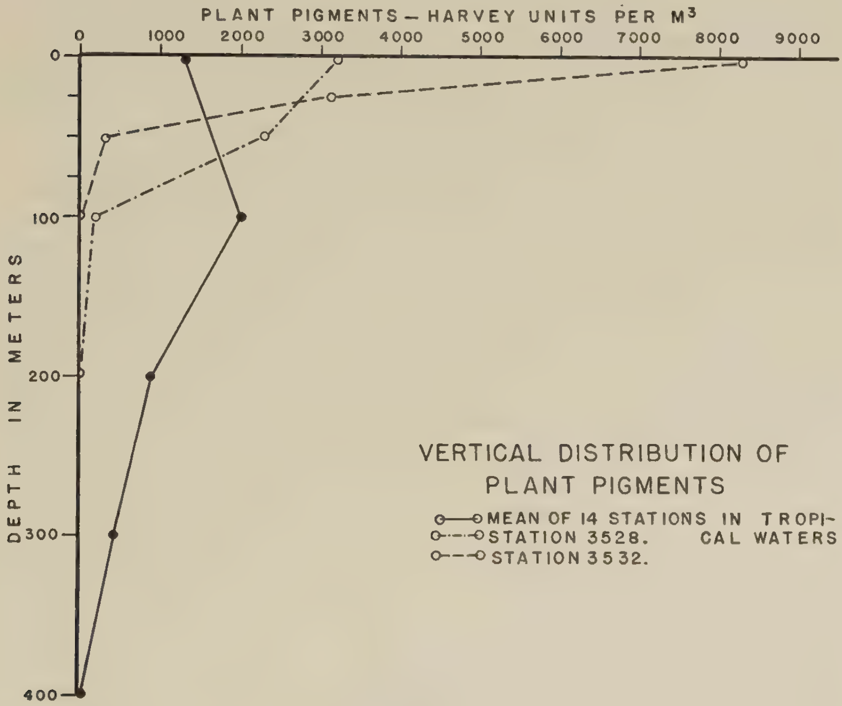


Figure 50. Vertical distribution of plant pigments.

mean being 310,000 units per m^2 and the smallest observed value 235,000 units.

This result appears rather anomalous in view of the prevalent belief that the quantity of plankton in tropical waters is much smaller than that in temperate regions. Lohmann's data on centrifuge plankton (1920), conveniently summarized by Harvey (1928) in tabular form, show a mean annual crop of 500 to 600 cells per liter in the upper 400 m. in latitudes 0° to 30° N, 2000 cells per liter from 30° to 40°, and 6000 cells from 40° to 50°. Differences in the net plankton are still more marked.

It should be pointed out that the northern waters were approaching summer conditions at the time the present analyses were made. A study of the seasonal cycle, including the spring and autumn blooms, would probably give a higher average for the northern waters. Nevertheless, the two seasonal studies that are available for direct comparison do not change the general picture. In the English Channel in 1934 (cf. Harvey, Cooper, Lebour, and Russell, 1935), the mean standing crop during the spring months was 1800 units per m^3 in the upper 45 m., or 81,000 units per m^2, and the largest observed crop was about 160,000 units. Thus not only was the spring bloom considerably smaller than the average obtained for tropical waters when calculated on an absolute areal basis, but also the mean crop per unit volume was only 1.4 times as large, and the mean for the entire year was slightly smaller.

In a study of Long Island Sound, the mean of sixty chlorophyll analyses during the period from September 2, 1938 to July 28, 1939 was 18.3 mgs. per m^3 at the surface and about 370 mgs. per m^2. The chlorophyll at the fourteen stations in tropical waters, estimated on the basis of the chlorophyll-plant pigment ratio at the surface, was probably about 270 mgs. per m^2, and thus was only slightly less than the crop in Long Island Sound.

While the data presented here are hardly sufficient to permit definite conclusions, it is evident that the generalizations that have previously been made about the regional aspects of plankton and productivity are open to suspicion. More detailed work is needed, for the discrepancies noted here might easily be accounted for on the basis of differences in nutrient supply dependent on seasonal and local variations in physical conditions.

NUTRIENTS

The distribution of nitrate and phosphate is summarized in Figure 51. The vertical distribution of nitrate shows a close inverse relation with the quantity of plant pigments. The minimum is at 100 m. in the southern waters and at the surface in the north, where the maximum quantities of phytoplankton occur, and the increase in nitrate becomes marked at the point of extinction of plant pigments, except in the two northern deep water stations, where the nitrate remains relatively low at 100 m. in spite of the fact that there is little phytoplankton there. But the slightly higher temperatures at 100 m. indicate that there are disturbing physical factors, probably intrusion of southern water. The inverse relation of phosphate with plant pigments is discernible but not particularly striking.

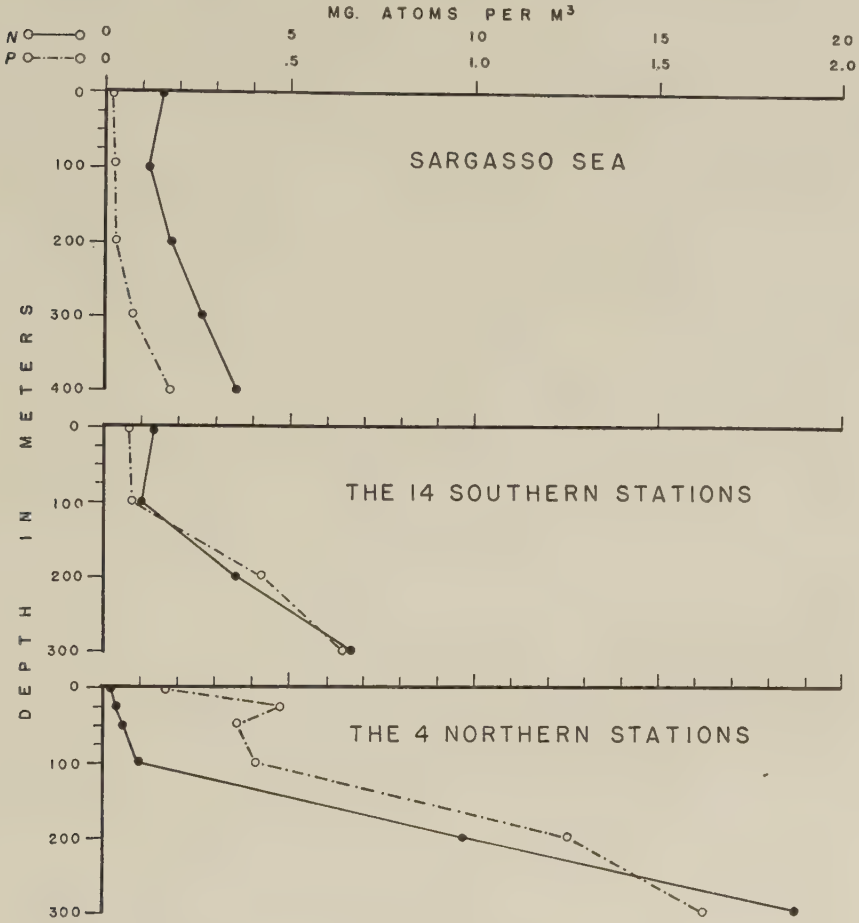


Figure 51. Vertical distribution of nitrate and phosphate.

The mean $N:P$ ratios of all the southern stations approach the normal value of 15 : 1 (Cooper, 1938). In the Sargasso Sea, however, the phosphates were very low, sometimes undetectable. In the northern waters, on the other hand, the nitrates were relatively low, with a strong negative anomaly of nearly 14 at the surface, decreasing to 3 at 300 m. This may have been a seasonal phenomenon, due to the fact that the phosphate generally is regenerated more quickly than nitrate after the spring bloom.

OXYGEN AND NITRATE EXPERIMENTS

The experimental values for oxygen and nitrate production and consumption are shown in Table II.

TABLE II

Oxygen and Nitrate Experiments

Station	*Oxygen production*	*Oxygen consumption*	*Nitrate consumption*	*Decrease in N Light bottle*	*Decrease in N Dark bottle*
3486......	.04	.12	.05	.25	.20
3491......	.20	.23	.00	.43	.43
3492......	.09	.17	.00	.13	.13
3498......	.07	.16	.03	−.40	−.43
3500......	.03	.03	.00	.20	.20
3510......	.21	.18	.00	.03	.03
3511......	.15	.09	−.07	−.27	−.20
3512......	.07	−.01	−.16	.34	.50
3513......	.16	.17	.08	−.49	−.57
3514......	.03	.06	.06	.56	.50
3515......	.04	.04	.12	.09	−.03
3517......	.05	.14	.00	1.00	1.00
3520......	.09	.14	.02	.18	.16
3523......	.05	.13	.05	.20	.15
3528......	.12	.10	−.55	−.60	−.05
3532......	.33	.32	.00	.00	.00
3535......	.12	.14	1.10	.15	−.95
3537......	.15	.05	−.05	.05	.10

Oxygen production and consumption recorded as mgs. per liter per day; nitrate as mg. atoms of *N* per m^3 per day.

The mean oxygen production—the difference between the oxygen content of light and dark bottles at the end of the experiment—was 0.111 mg. per liter per day. At the four stations in northern waters the mean was 0.180 mg.; in the southern waters it was 0.091 mg. Thus the ratio for oxygen production in the two areas is about the same as the chlorophyll ratio.

The mean of all the analyses of the Tortugas region, described in the first paper of this series, was 0.187 mg. per liter per day, and the average for Station 2, which gave more reliable results, was 0.131 mg. This suggests that the production per unit volume at the surface is somewhat greater in the tropical shallows than in areas of greater depth, but the difference is not very marked. It is apparently considerably greater in northern shallows. Gran (1927) estimated that the mean production in the coastal waters off Bergen was 0.37 mg. per liter per day during the spring bloom of 1922, and Marshall and Orr obtained a value of 0.43 mg. in Loch Striven in April, 1926. The mean of sixty analyses in Long Island Sound between September, 1938, and July, 1939, was 0.461 mg. per liter per day.

Unfortunate circumstances prevented attempts to measure oxygen production throughout the entire euphotic zone. But in view of the scarcity of evidence on oceanic plankton production, it seems desirable to attempt a rough estimate of production in the areas examined, even though the error of such an estimate may be rather large.

The curve for oxygen production against depth may be characterized as increasing slightly from the surface to the point of optimum light intensity and then decreasing exponentially to the limit of photosynthetic activity, which is generally located where the light is about 0.5 to 1% of the incident radiation. In northern waters the optimum light intensity is at about 5 m. (Jenkin, 1937, and others). In the Sargasso Sea, Clarke (1936) found that the optimum for a culture of *Nitzschia closterium* was 80 m. The optimum for the normal Sargasso plankton is probably higher, for in the Tortugas region, in which the water is only slightly less transparent (cf. Taylor, 1928, and Darby, Johnson, and Barnes, 1937), it was found to be between 10 and 15 m. The limit of photosynthesis is probably about 50 m. in the northern waters and 150 m. in the south, these figures being in accordance with the data on light penetration and such evidence as is available for photosynthetic activity (Clarke, 1936; Clarke and Oster, 1934).

Curves for the sixteen deep water stations were drawn by extending the known surface value downward (since the real maximum is unknown) to a depth of 5 m. at the northern stations and 15 m. at the southern ones, with an exponential decrease thereafter to 1% of the surface value at 50 and 150 m. respectively. At Station 3537, with a depth of 38 m., the limit was placed at that depth, and at station 3500 the production was assumed to be uniform from surface to bottom (17 m.). The curves were integrated planimetrically, and the mean for the thirteen southern deep water stations was found to be 0.42 mg. of oxygen per cm^2 per day. The average for all the southern stations was 0.39 mg. At Station 3537 the estimated production was 0.16 mg., and the mean for the other three northern stations was 0.25, giving a general average of 0.23 mg. This would be equivalent to a production of 0.142 g. of oxygen per cm^2 per year in the southern waters and 0.084 g. in the north, representing an annual fixation of 0.053 and 0.032 g. of carbon respectively. Although such estimates can be regarded as little better than guesses, it is interesting to note that they are of the same order of magnitude as the estimate of 0.0278 g. of carbon which Seiwell (1935) obtained by measuring the oxgyen deficit of the western Atlantic between 3° and 13° N.

In comparing the oxygen production of northern and southern waters, the conclusion appears to be about the same as that which was reached in the comparison of the standing crops. The production at the surface is slightly greater in the north, but the euphotic zone is undoubtedly thicker in the south. The total production per unit area was probably somewhat greater in the southern waters during the particular time the analyses were made. Inclusion of bloom periods would lessen the difference, but even with six months of bloom conditions, with values of about 0.4 mg. of oxygen per liter per day, which seem to be normal for temperate regions, the annual production in the northern area probably would not be significantly greater than in the south.

Obviously such estimates cannot be regarded as critical evidence until much more is known about the variations of photosynthetic activity with depth. Nevertheless, the available data tend toward confirmation of Seiwell's contention, in the paper referred to above, that the tropical waters are not relatively unproductive.

The correlation of oxygen production with chlorophyll is .514, and with total plant pigments it is .614. These correlations are statistically significant, and the variations in the standing crop account for about 55% of the variations in the gross production of glucose. None of the other factors examined—temperature, nitrate, or phosphate—appear to be significant, but there are complications in the statistical treatment which make it appear that the result is due not to a lack of relationships but to complex inter-relationships that cannot be evaluated properly at the present time.

The mean oxygen consumption was 0.118 mg. per liter in the tropical waters and 0.152 mg. at the northern stations. The average of all the analyses was 0.126 mg. per liter. Such large values, particularly in the southern waters where the mean consumption was greater than the production, make it appear unlikely that the values have much significance. It is probable that the well known phenomenon of the multiplication of bacteria in stored seawater (ZoBell and Anderson, 1936, and others) causes a consumption of oxygen that is greater than normal. This viewpoint is supported by the fact that the relationship between plant pigments or chlorophyll and oxygen consumption is slight. The regression equation for all the analyses in southern waters, calculated according to the products moments method, is

$$X = 0.0088Y + 107$$

where Y is Harvey units of plant pigments per m^3 and X is milligrams of oxygen consumed per m^3 per day. The equation gives a mean value for oxygen consumption by phytoplankton of 11 mgs. per day, or 9% of the total. But according to the probable error of the relationship, the constant for Y may have a variation of ± 0.0064, so that the statistical estimate lies somewhere between 1% and 17% of the total consumption.

When the equation is applied to the entire vertical column, the estimate for total phytoplankton respiration is 0.30 ± 0.22 mg. per cm^2 per day. This is a maximal value because the equation is not strictly applicable to respiration at the reduced temperatures found in the lower part of the column. Even so, it appears to be somewhat less than the estimate for total production, which was 0.42 mg. A smaller value is to be expected since the production is theoretically equivalent to respiration plus the oxygen equivalent of organic matter lost from the phytoplankton crop (animal consumption, sinking, etc.).

The number of analyses of northern waters is not sufficient for statistical treatment. Nor is it considered valid to attempt an indirect estimate by treating all the data together, because the wide variation of other factors—temperature, animals, and perhaps bacteria—introduce complex interrelationships that cannot be analyzed accurately with the data available.

The nitrates were determined in the experimental bottles because it was believed that they would provide valuable supplementary evidence on plankton growth. Theoretically, the nitrate consumption—i.e., the difference between the nitrate in the light and dark bottles—can be used to measure production in the same way as the oxygen content, although it is a minimal estimate because there are other forms of nitrogen available, and the results of the two determinations are not quite analogous because the nitrate consumption is obviously a measurement of the formation of protein and other nitrogenous substances rather than glucose.

The results of the experiments, however, are difficult to interpret. There was generally a decrease in the light bottles, averaging 0.10 mg. atom per m^3 per day, but in the dark bottles there was also a decrease, amounting to 0.06 mg. atom. The mean difference between the two—the so-called nitrate consumption—was 0.038 mg. atom.

Without determining the cause of the decrease of nitrate in twelve of the eighteen dark bottles, it is impossible to progress very far with the evaluation of the results. If it were caused by bacterial activity, which might be expected to proceed at an equal rate in both light and dark bottles, the value of 0.038 mg. atom would represent the activity of the phytoplankton. If, on the other hand, the decrease were caused by phytoplankton absorption in the dark, which is known to occur in experiments with pure cultures, with the removal of both nitrate (Ketchum, 1939) and phosphate (Harvey, 1933; Ketchum, 1939), the decrease in the light bottle would be a better estimate of the total utilization by phytoplankton, but it would be minimal because it would take no account of normal bacterial regeneration.

Regardless of which estimate is preferred, there appears to be a discrepancy between the results of the nitrate and oxygen experiments. A nitrate consumption of 0.038 to 0.10 mg. atom per m^3 per day would represent a daily plankton production of 7.6 to 20 mgs. of organic matter with a normal nitrogen content of about 7%. With a mean oxygen production of 0.111 mg. per liter per day, 104 mgs. of glucose would be produced per m^3. About ten percent appears to be used up in normal respiratory processes, and the remainder, 94 mgs., is available for transformation into plankton. This would constitute a daily production of 75 mgs. of organic matter with the usual carbon content of about 50%. The phytoplankton production as measured by the nitrate consumption is therefore only 10% to 27% as great as the oxygen production would suggest.

Such a discrepancy might be due to errors in the experimental technique or variations in the factors involved in the estimates. On the other hand, it might be caused by the failure of the phytoplankton to utilize much of the carbon produced, with a resultant accumulation of large stores of foodstuffs. The experimental evidence is not complete enough to throw any light on the matter; however, the work on Long Island Sound, referred to above, is of interest in this respect, for although it neither confirms nor rejects the first possibility, it helps to clarify the second.

In the first place, on numerous occasions a significant increase in chlorophyll has been observed in the dark bottles (this is in accord with the results of Harvey, who found an increase in both plant pigments and cells; Ketchum has not detected an increase). In the Sound, this phenomenon may occur during periods when the quantity of nutrients has suddenly risen after having been at a low level for some time, and it is also common in the winter when the nutrient content is fairly high but the temperature is low. Such an increase is generally accompanied by a diminution or reversal of the normal processes of regeneration of *N* and *P* in the dark bottles. It is therefore evident that in the natural plankton association, as well as in laboratory experiments with pure cultures, the fixation of carbon and its conversion to protoplasmic substances are not necessarily coincident processes. The second may lag behind the first when physical or chemical conditions are not favorable for conversion. It is therefore hardly to be expected that the results of experiments on oxygen production and nitrogen consumption should coincide. When the Long Island Sound data on phytoplankton production are calculated in the way described above, the ratio of nitrate consumption to oxygen production varies from a negative value to about 110%, and the mean is 38%. The higher average here suggests that the Sound, with its greater concentration of nutrients, is less conducive to such phenomena than oceanic areas.

It is obvious that there is a limit to the amount of stored foodstuffs that a plant can accumulate. But if, as the calculations suggest, active photosynthesis at the surface for one day supplies the normal respiratory requirements for ten days, the phenomenon is likely to be important, for not only does it provide a mechanism for carrying the plant through periods of unfavorable nutritive conditions, but also it permits a lengthy existence as well as assimilation and growth below the euphotic zone. The latter would permit utilization of nutrients throughout a much longer column of water than is generally supposed, but whether this would increase or decrease the total productivity of the region would depend on the amount of turbulence. This and other ramifications of the theory suggest that it is a profitable subject for investigation.

ZOOPLANKTON

The zooplankton was collected in nets of No. 10 bolting silk, and the use of Clarke plankton samplers permitted the quantitative measurement of the amount of water strained. The results of the measurements are shown in Table III.

TABLE III

ZOOPLANKTON

Station	*Depth*	*Volume cc/m³*	*Nauplii and copepodites No./m³*	*Copepods No./m³*	*Misc. No./m³*	*Total No./m³*	*Total No./m²*
3486	0–150	0.02	130	230	20	380	116000
	150–300	0.02	160	200	30	390	
3492	0–100	0.05	160	700	90	950	95000
3511	0–150	0.07	240	760	50	1050	257000
	150–300	0.02	220	380	60	660	
3535	0–50	4.3	19000	29300	1500	49800	2490000
3537	0–25	8.1	5090	4580	2700	12370	309300

The counts are probably a more accurate estimate of the quantity of zooplankton than the volumes. The latter are distorted by the presence of enormous numbers of Ceratium and peridinians in the northern waters. The counts are also somewhat distorted, due to the usual qualitative variations. The miscellaneous groups in the southern waters, chiefly Sagitta, medusae, and decapod crustacean larvae, bulk larger than their number would indicate, but this is at least partly compensated by the larger average size of the northern copepod fauna, of which Calanus was a common constituent. When such small quantities of data are involved, such errors as these are generally of less importance than the sampling errors, and elaborate calculations of volume are not justified.

The number of animals per unit volume in the southern waters was about half as great as in the shallow waters of the Tortugas region. The latter were surface water determinations, and with more adequate sampling the difference might be more marked. But since the plankton in the deeper water occupies a long vertical column, showing little diminution down to the 300 m. level, there is little doubt that the total crop of zooplankton is much greater in the open ocean than in the shallow areas.

The number of animals per unit volume in the southern waters was from 0.8% to 8.5% as great as in the northern shallows, represented by stations 3535 and 3537. The total crop per unit area, down to the limit of sampling, was 3.8 to 83% as great. It therefore appears that the northern waters, in which the total standing crop of phytoplankton and the total productivity are less than in the south, and in which the crop per unit volume is only two or three times as great, may support a considerably larger fauna. It is impossible to say whether such a conclusion is rational. It depends on the food requirements at different temperatures, feeding efficiency with different concentrations of food in the medium, and other matters too poorly understood at present to permit quantitative expression. Qualitatively, however, it may be stated a priori that the food requirements are greater in tropical waters, so that a larger crop of phytoplankton is needed to support a given number of animals. Moreover, the rate of turnover may be faster, in which case the comparison of relative abundance would not be an accurate statement of the zooplankton productivity.

Finally, it is of interest to note that Harvey, Cooper, Lebour, and Russell (1935) found in the English Channel an annual mean of between 2000 and 3000 animals per m^3 in the upper 45 m., and Russell (1934) reported that the number of animals in the Great Barrier Reef lagoon is approximately equal to the crop in the North Sea and the English Channel. The figures listed by Harvey and his associates give a total crop of 90,000 to 135,000 animals per m^2, which is of the same order of magnitude as the number found in the southern waters in the present work. It therefore is possible that the zooplankton content of these waters was not relatively low, but rather that the quantity in the northern shallows was unusually large, either because of high productivity or perhaps because the samples were taken during a peak period.

SUMMARY

1. Measurements were made of temperature, oxygen, plant pigments, phosphate and nitrate at eighteen stations in the western North Atlantic between the northern coast of Cuba and Woods Hole during May and the early part of June, 1939. In the surface water of all stations the chlorophyll content was determined, and analyses were made of the oxygen and nitrate production and consumption in experimental light and dark bottles.

2. The quantity of plant pigments at the four northernmost stations was greatest at the surface, and the maximum depth of occurrence was 100 m. or less. At the southern stations they occurred to a depth of 300 to 400 m. or

more, and the maximum observed values were at 100 m. The quantity of plant pigments in the surface water was three times as great in the north as in the south, and the amount of chlorophyll was twice as great. But the total crop in the entire vertical column was considerably greater in the southern waters.

3. The mean oxygen production in the northern waters was 0.180 mg. per liter per day, about half as much as the values recorded by previous workers for temperate shallow-water regions during the spring bloom. In the tropical waters the average was 0.091 mg. Fifty-five percent of the variations in oxygen production can be accounted for on the basis of differences in the quantity of the standing crop. Other factors—temperature, light, and nutrients—did not appear to have a significant effect. Although the gross productivity (glucose production) of the southern surface waters is only half as great as in the north, it is suggested that because of the greater transparency of the water, the maximum depth of photosynthesis is about three times as great, and the total productivity per unit area may be equal to or greater than that of temperate regions. Nitrate consumption was relatively much less than oxygen production, and rough estimates indicate that only 10 to 27% of the glucose produced was transformed into nitrogenous material during the course of the experiments. The theoretical biological implications of this phenomenon are discussed.

4. Quantitative measurements of zooplankton were made at five stations. The total number of animals was less in the tropical waters than at the northern stations but was about equal to the annual mean for certain other temperate regions, the English Channel and the North Sea, as well as the tropical waters of the Great Barrier Reef lagoon.

REFERENCES CITED

1. Atkins, W. R. G.
1932. Nitrate in sea water and its estimation by means of diphenylbenzidine. J. Mar. Biol. Assoc. *18:* 167–192.

2. Clarke, G. L.
1936. Light penetration in the western North Atlantic and its application to biological problems. Cons. Perm. Intern. l'Explor. Mer. Rapp. Proc. Verb. *101* (2): 3–14.

3. Clarke, G. L., and Oster, R. H.
1934. The penetration of the blue and red components of daylight into Atlantic coastal waters and its relation to phytoplankton metabolism. Biol. Bull. *64:* 59–75.

4. Cooper, L. H. N.
1938. Salt error in determinations of phosphate in sea water. J. Mar. Biol. Assoc. *23:* 171–178.

5. Cooper, L. H. N.
1938a. Redefinition of the anomaly of the nitrate-phosphate ratio. J. Mar. Biol. Assoc. *23:* 179.

6. DARBY, H. H., JOHNSON, E. R. F., AND BARNES, G. W.
1937. Studies on the absorption and scattering of solar radiation by the sea. Papers Tortugas Lab. Carn. Institution Wash. *31:* 191–205.

7. GRAN, H. H.
1927. The production of plankton in the coastal waters off Bergen. March–April, 1922. Rep. Norweg. Fish. Mar. Invest. *3* (8).

8. HARVEY, H. W.
1928. Biological physics and chemistry of sea water. Cambridge Univ. Press.

9. HARVEY, H. W.
1933. On the rate of diatom growth. J. Mar. Biol. Assoc. *19:* 253–275.

10. HARVEY, H. W., COOPER, L. H. N., LEBOUR, M. V., AND RUSSELL, F. S.
1935. Plankton production and its control. J. Mar. Biol. Assoc. *20:* 407–441.

11. JENKIN, P. M.
1937. Oxygen production by the diatom *Coscinodiscus excentricus* Ehr. in relation to submarine illumination in the English Channel. J. Mar. Biol. Assoc. *22:* 301–343.

12. KETCHUM, B. H.
1939. The development and restoration of deficiencies in the phosphorus and nitrogen composition of unicellular plants. J. Cell. Comp. Physiol. *13:* 373–381.

13. KIMBALL, H. H.
1928. Amount of solar radiation that reaches the surface of the earth on the land and on the sea, and the methods by which it is measured. Monthly Weather Rev. *56:* 393–398.

14. LOHMANN, H.
1920. Die Bevölkerung des Ozeans mit Plankton u. s. w. Arch. f. Biontologie *4* Heft 3. Berlin.

15. MARSHALL, S. M. AND ORR, A. P.
1930. A study of the spring diatom increase in Loch Striven. J. Mar. Biol. Assoc. *16:* 853–878.

16. RILEY, G. A.
1938. Plankton studies. I. A preliminary investigation of the plankton of the Tortugas region. J. Mar. Res. *1:* 335–352.

17. RUSSELL, F. S.
1934. A comparison of the abundance of zooplankton in the Barrier Reef lagoon with that of some regions in northern European waters. Brit. Mus. Nat. Hist. Great Barrier Reef Exped. Sci. Rep. *2:* 176–185.

18. SEIWELL, H. R.
1935. The annual organic production and nutrient phosphorus requirement in the tropical western North Atlantic. J. Cons. *10:* 20–32.

19. TAYLOR, W. R.
1928. The marine algae of Florida with special reference to the Dry Tortugas. Papers Tortugas Lab. Carn. Inst. Wash. *25:* 1–219.

20. ZOBELL, C. E., AND ANDERSON, D. Q.
1936. Observations on the multiplication of bacteria in different volumes of stored sea water and the influence of oxygen tension and solid surfaces. Biol. Bull. *71:* 324–342.

TABLE IV

Station List and Analyses

	Depth	Temp.	Oxygen cc./l.	Oxygen % sat.	P mg. at. per m^3	N mg. at. per m^3	Plant pigments Harvey units/m^3	Chlorophyll mgs./m^3
Station 3486								
5/11/39	1	26.63	4.68	99	0.18	1.00	3500	2.5
23° 13′ N, 81° 22′ W	100	25.87	4.56	95	0.09	0.50	3400	
Depth 722 m.	200	20.64	4.40	84	0.44	2.21	1800	
Station 3491	1	26.93	4.72	100	0.03	1.70	2000	1.5
5/15/39	100	25.37	4.43	92	0.06	0.31	1200	
23° 44′ N, 81° 46′ W	200	19.26	3.54	66	0.29	0.93	900	
Depth 1719 m.	300	16.82	3.78	67	0.59	14.3	600	
Station 3492	1	26.77	4.66	99	0.06	0.62	1400	0.9
5/16/39	48	24.41	4.88	100	0.05	0.62	1700	
25° 14′ N, 80° 05′ W	97	21.14	4.63	89	0.08	1.18	2900	
Depth 230 m.	184	10.40	2.90	46	1.82	18.2	700	
Station 3498	1	26.67	4.67	99	0.16	0.57	1700	1.3
5/21/39	98	25.26	4.45	92	0.09	0.36	2100	
25° 49′ N, 79° 35′ W	197	18.19	3.60	66	0.45	1.65	1600	
Depth 777 m.	296	14.27	2.91	50	1.08	9.1	1300	
Station 3500	1	26.66	4.63	98	0.14	2.00	1900	1.6
5/21/39								
25° 33′ N, 79° 19′ W								
Depth 17 m.								
Station 3510	1	26.38	4.67	98	0.04	0.10	900	0.9
5/23/39	94	22.31	4.78	96	0.00	0.00	2000	
26° 48′ N, 79° 47′ W	188	12.48	3.17	52	1.45	6.5	900	
Depth 357 m.	282	7.96	2.90	44	1.93	23.4	700	
Station 3511	1	26.31	4.60	97	0.16	1.80	800	0.7
5/24/39	87	24.06	4.42	90	0.17	1.34	2500	
31° 02′ N, 79° 18′ W	173	20.18	3.41	65	0.61	2.52	700	
Depth 732 m.	260	16.87	3.45	62	0.90	3.86	100	
Station 3512	1	26.53	4.54	96	0.00	2.42	900	0.6
5/25/39	100	24.31	4.06	82	0.12	2.21	2300	
33° 10′ N, 76° 34′ W	200	19.48	4.35	81	0.22	4.88	900	
Depth 704 m.	300	17.79	4.58	83	2.05	5.70	300	
Station 3513	1	23.98	5.00	101	0.02	0.67	700	0.5
5/26/39	100	20.68	5.02	96	0.05	0.15	1800	
34° 15′ N, 73° 11′ W	200	18.99	4.76	88	0.00	0.46	1000	
Depth 4471 m.	300	18.09	4.73	86	0.17	0.21	300	
Station 3514	1	21.99	5.22	102	0.00	2.00	1300	0.8
5/27/39	97	18.12	5.19	95	0.00	2.11	2200	
34° 48′ N, 69° 53′ W	193	17.96	5.13	94	0.02	3.96	1300	
Depth 5276 m.	290	17.82	5.03	91	0.05	2.83	400	
	386	17.42	4.59	83	0.29	7.0	<100	
Station 3515	1	22.90	5.10	101	0.01	0.87	800	0.6
5/28/39	97	19.67	5.09	95	0.01	0.98	1500	
35° 10′ N, 66° 50′ W	193	18.39	5.13	94	0.01	1.28	200	
Depth 5148 m.	290	18.09	5.17	94	0.04	4.57	200	
	386	18.11	5.19	95	0.08	1.64	100	
Station 3517	1	22.05	5.22	102	0.00	3.44	600	0.4
5/29/39	100	18.32	5.12	94	0.07	1.80	1500	
35° 54′ N, 67° 34′ W	201	18.02	5.06	92	0.04	2.05	400	
Depth $>$ 4000	301	17.67	4.92	89	0.12	4.57	200	
	402	17.18	4.72	85	0.24	2.42	<100	

TABLE IV—*Continued*

STATION LIST AND ANALYSES

	Depth	Temp.	Oxygen cc./l.	Oxygen % sat.	P mg. at. per m³	N mg. at. per m³	Plant pigments Harvey units/m³	Chlorophyll mgs./m³
Station 3520	1	23.14	5.02	100	0.04	0.67	900	0.7
5/30/39	100	19.40	5.04	94	0.00	1.03	1500	
37° 02′ N, 68° 43′ W	201	18.23	5.16	94	0.04	0.77	500	
Depth >4000	301	18.10	5.18	94	0.00	0.82	400	
	402	17.81	4.87	88	0.10	3.24	100	
Station 3523	1	25.10	4.90	101	0.03	0.46	800	0.6
5/31/39	102	21.47	4.44	86	0.07	1.44	1200	
37° 49′ N, 69° 18′ W	203	18.47	4.37	80	0.10	0.67	1000	
Depth >4000	305	17.13	4.17	75	0.20	1.13	300	
	407	14.84	3.72	64	1.01	8.8	100	
Station 3528	1	19.67	5.53	102	0.05	0.10	3200	1.4
6/1/39	45	14.35	5.54	94	0.12	0.46	2300	
38° 51′ N, 70° 04′ W	91	14.47	5.26	89	0.29	0.62	200	
Depth 2963 m.	181	13.08	4.32	71	1.17	8.6	<100	
	272	10.69	3.24	51	1.62	18.8	<100	
Station 3532	1	11.95	6.86	111	0.25	0.10	8300	3.6
6/2/39	23	10.20	6.15	96	0.45	0.41	3100	
39° 51′ N, 70° 53′ W	45	11.45	5.87	94	0.40	0.31	300	
Depth 969 m.	91	11.90	5.35	86	0.53	1.28	<100	
	181	11.41	5.30	58	1.35	10.8	<100	
Station 3535	1	10.63	7.05	111	0.15	0.26	1700	1.2
6/2/39	25	8.55	7.65	115	0.18	0.15	2700	
40° 22′ N, 71° 21′ W	50	6.64	6.53	95	0.57	0.87	700	
Depth 82 m.								
Station 3537	1	12.52	6.63	108	0.20	0.31	3300	2.0
6/3/39	10	10.61	7.23	114	0.13	0.41	3300	
40° 52′ N, 71° 50′ W	25	5.84	6.01	86	0.80	0.41	3200	
Depth 38 m.								

Contribution No. 233

Vol. VII, Art. 2

YOUNG CARANX IN THE WESTERN NORTH ATLANTIC*

By J. T. Nichols
American Museum of Natural History

Through the courtesy of Dr. A. E. Parr of the Peabody Museum, Yale University, I have recently had the privilege of studying young fishes of the genus *Caranx* in the Bingham Oceanographic Collection, obtained off shore in the western North Atlantic, 1927 to 1934. The five species characteristic of the West Indian fauna are represented as follows:

CARANX RUBER (Bloch)

Of this species there is one specimen 25 mm. in standard length from the Caribbean south of Haiti in late March (Atlantis, 1933); one 23 mm. standard length, 5 of 28 to 48 mm., 2 of 52 and 62 mm., with 1 *bartholomaei* from the Windward Passage south of Guantanamo Bay, April 17 to 18 (Atlantis, 1933, surface); 5, 21½ to 25 mm. standard length, 33 of 26½ to 49 mm., 2 of 54 and 57 mm., with one small *bartholomaei,* Misteriosa Bank to Yucatan, April 11 (Atlantis, 1933). With this Caribbean series are 2, 21 and 35 mm. standard length, with 19 *bartholomaei* and one small *crysos* (Atlantis, 1934), presumably from 14° 42′ N., 79° 18′ W., Feb. 19, but place and date uncertain.

There are 32 specimens 14 to 26 mm. standard length, 1 of 34 mm., Havana to New York, May 10 to 15 (Mabel Taylor, 1932); 7 specimens 13 to 25 mm. standard length, 7 of 28 to 48 mm., with 33 *crysos,* from the mid-Gulf Stream, 38° 07′ N., 68° 45′ W. to 37° 12′ N., 67° 39′ W., August 21 to 22 (Atlantis, 1934).

Distribution

Grown *Caranx ruber* are rather common about Cuba and Bermuda, plentiful in Haiti and the Bahamas, not plentiful about Porto Rico, occur in small numbers only in southern Florida, and are rare north of there on the mainland. Their preferred habitat seems to be islands and reefs.

The young are occasional but only occasional in the Carolinas (Natural History [N. Y.], 1935, XXVI, p. 268). I have recently examined one of 66 mm. standard length from sargassum off Charleston sent me by Mr. E. Milby Burton; but their habitat was unknown to me until they were found common in the Gulf Stream off Bimini in July, 1937, and a series from there of 34 measuring 17.5 to

---

* Joint contribution from Woods Hole Oceanographic Institution (No. 233), American Museum of Natural History and Bingham Oceanographic Foundation.

30 mm., and 9 from 31 to 43 mm. was examined (Copeia, 1937, no. 4, pp. 236–237). The Gulf Stream is obviously their Atlantic nursery ground. That they are not more frequent between it and the continent may be due to their entering mainly from its easterly edge, or perhaps they frequent the current rather than slack waters at the edges until large enough to migrate independently, when they must of necessity strike southward or be lost.

In the Caribbean young *Caranx ruber* are evidently more advanced at an earlier date. They are abundant between Cuba and Yucatan, and perhaps more generally distributed than in the Atlantic. It is suggested that high water temperatures may determine the distribution of young of this species.

Descriptive Notes

From this extensive series we have change of proportions of young as follows. Fifteen specimens of 13 to 19 mm. standard length have depth in same 2 to 2.2 (average 2.05); 32 of 20 to 26 mm., 2 to 2.4 (average 2.18); 11 of 26½ to 30 mm., 2.2 to 2.5 (average 2.35); 20 of 32 to 39 mm., 2.4 to 2.6½ (average 2.49); 16 of 41 to 49 mm., 2.5 to 2.9 (average 2.59); 4 of 52 to 62 mm., 2.7 to 2.9 (average 2.77½). These measurements show a somewhat greater depth than those of a smaller series taken in the Gulf Stream in 1937 (Copeia, 1937, l. c.). There is variation at the size at which depth begins to fall off noticeably in *C. ruber*. Although for the most part less deep than young *bartholomaei* at any size, material of this last to hand shows some overlap at lengths from 20 to 30 mm. The smallest *bartholomaei* with depth in length as much as 2 is 20 mm., the largest *ruber* with depth in length as little, 21½ mm. An exceptional *bartholomaei* has depth as much as 2.3 at 29 mm., the largest *ruber* with depth as little as 2.3 is 30 mm. Presumably the depth of both species falls off irregularly at about this critical size, a tendency which soon fades in the deep-bodied *bartholomaei*, and accelerates in the slender *ruber*.

The pectoral of these Atlantic young *ruber* is noticeably more lengthened at corresponding small sizes before it definitely begins to elongate, than that of the Caribbean young. Thus in 39 Atlantic specimens from 13 to 26 mm. standard length, pectoral in head measures 1.4 to 1.8 (average 1.55); in 5 of 28 to 36 mm., 1.5 to 1.6 (average 1.54); in 3 of 43 to 48 mm., 1.4 to 1.5 (average 1.43). In 8 Caribbean specimens of 21 to 25 mm. it measures 1.5 to 1.8 (average 1.62½); in 26 of 26½ to 39 mm., 1.5 to 1.8 (average 1.63); in 17 of 41 to 62 mm., 1.3½ to 1.5 (average 1.45). This is not a geographic difference between Atlantic and Caribbean young, however, seen by comparing the same measurement in 39 specimens from the Gulf Stream off Bimini taken in 1937. In 22 of 17½ to 25 mm. it is 1.5 to 2.2 (average 1.72); in 16 of 27 to 35 mm., 1.5 to 2 (average 1.69); in one of 43 mm., 1.4. The series seem too large for these differences to be mere matters of chance, and they are presumably inherent in different lots of fishes, or induced by different environmental conditions.

The material is mostly too faded to show more than traces of the color pattern which is never bold in small *C. ruber*. The spinous dorsal is no more than gray where it tends to be blackish in *bartholomaei*, the ventrals pale instead of frequently dusky. Indistinct narrow pale cross streaks are occasionally present, and an exceptional specimen of 23 mm. has 6 distinct though faint narrow dark crossbands slightly wider than pale interspaces, from the front of the spinous dorsal to the last quarter of the soft dorsal, about one more than *bartholomaei* when similarly banded. Traces of the diagnostic dark stripe on the lower caudal lobe are usually present in the larger specimens (45 mm. and over), if only as an appreciable smudge diagonally across the peduncle,—and may occasionally be seen in specimens down to 29 mm. There are specimens of 20 to 30 mm., only to be differentiated from *C. bartholomaei* by more numerous gill-rakers on the lower limb of the first arch, upwards of 25 may be counted versus never more than 20.

CARANX BARTHOLOMAEI Cuvier and Valenciennes

There are specimens of this species taken at various scattered dates and localities mostly in the Caribbean, but the only considerable number, 19 specimens, 6 of 17 to 23 mm. standard length, 9 of 29 to 44 mm., with 2 *ruber* and one small *crysos* (Atlantis, 1934) are presumably from 14° 42′ N., 79° 18′ W., Feb. 19, but place and date uncertain; 3 of 27 to 30 mm. are from 13° 33′ N., 80° 40′ W. to 15° 47′ N., 78° 48′ W., Feb. 18 to 20 (Atlantis, 1934, surface light at night). One specimen of 16 mm. is from 22° 12′ 55″ N., 74° 19′ W., March 31 (Pawnee, 1927, 4000 ft. wire); 2 of 22 and 26 mm. from 26° 25′ N., 69° 07′ W. to 21° 05′ N., 71° 25.5′ W., Jan. 26 to 28 (Atlantis, 1934); 1 of 20 mm., with 40 *ruber*, from Misteriosa Bank to Yucatan, April 11 (Atlantis, 1933); 1 of 51 mm., with 8 *ruber*, from Windward Passage south of Guantanamo Bay, April 17 to 18 (Atlantis, 1933, surface); 1 of 25 mm., Caribbean, Feb. 2 (Atlantis, 1934); 1 of 20 mm., Caribbean off Panama, mid-Feb. (Atlantis, 1934); and one other of 41 mm., Caribbean (Atlantis, 1934).

Distribution

Grown *Caranx bartholomaei* are rather common about Cuba and Bermuda, occur but in small numbers in southern Florida and are rare further north on our coast, though the species is reported in late summer and fall at Woods Hole, Mass. They are plentiful in the Bahamas and in Haiti, rather uncommon in Porto Rico.

When young this species is an inhabitant of drifting gulf weed. It has been found with weed in southern Florida, in the eastern edge of the Gulf Stream off Bimini, Bahamas, and is abundant with the weed in summer at Cape Lookout, North Carolina, apparently rare on the coast north of the Carolinas.

The significant thing about the species in this collection of young fishes is its small numbers almost everywhere, and its absence in the Gulf Stream. Presumably its nursery grounds are rather among stagnant weed, at or beyond the edge of the current. Though it might be assumed, as in the case of *ruber*, to enter the stream mostly on the east side, it is abundant on the west side as has been mentioned (Cape Lookout).

Descriptive Notes

For comparison with *Caranx ruber*, we have change of proportion of young as follows. Three specimens 16 to 19 mm. in standard length have depth 1.7 to 1.9 (average 1.80); 9 of 20 to 26 mm., 1.8½ to 2.1 (average 1.95); 5 of 27 to 30 mm., 2 to 2.3 (average 2.13); 6 of 31 to 40 mm., 2 to 2.2 (average 2.10); 2 of 41 and 44 mm., 2.1 and 2.2 (average 2.15); and one of 51 mm., 2.1.

The color pattern of these specimens is badly faded. One of 20 mm. standard length has dark cross-bands unusually well developed. It has 5 dark bands completely across the body, broader than the interspaces above, averaging equal to them below, and a slanting dark mark behind the eye; spinous dorsal and ventrals more or less dusky. The dark bands are less bold than in *hippos*. Various specimens have more or less dusky ventrals, particularly larger ones, though one of 16 mm. shows this character which distinguishes young *bartholomaei* from young *ruber*. It is probably not constant for *bartholomaei*, however, even in fresh material. Three or 4 show the slanting dark mark between nape and eye which is more characteristic of this species than of *ruber*. Eleven of the 26 specimens, ranging from 17 to 44 mm. standard length, show large indistinct pale spots or blotches irregularly covering the body (Amer. Mus. Novitates, 1937, No. 967, pp. 4–5). This pattern seems to be diagnostic of *bartholomaei*, a concealment adaptation to sargassum, and that nine of the series of 15 show it leads me to suppose that this series was taken in weed, though not specifically so labelled.

CARANX CRYSOS (Mitchill)

There is 1 specimen 18 mm. in standard length with 19 *bartholomaei* and 2 *ruber* (Atlantis, 1934), presumably from 14° 42′ N., 79° 18′ W., Feb. 19, but place and date uncertain; 20 of 13 to 25 mm., 12 of 28 to 43 mm., 1 of 72 mm., with 14 *ruber*, from 38° 07′ N., 68° 45′ W. to 37° 12′ N., 67° 39′ W., August 21 to 22 (Atlantis, 1934); 16 specimens, 10 of 12 to 26 mm., 4 of 28 to 48 mm., with 2 small *sexfasciatus*, from 36° 48′ N., 68° 55′ W. to 38° 59′ N., 69° 46′ W., August 27 to 28 (Atlantis, 1934, in sargassum).

Distribution

Grown *Caranx crysos* are plentiful in the Bahamas, from southern Florida to North Carolina, and occur northward to Cape Cod in summer. They are apparently also plentiful on the South American coast, less plentiful though generally distributed in the West Indies, Atlantic shore of the Isthmus, about

Cuba, Haiti, Porto Rico, uncommon at Bermuda. The identical species occurs in West Africa from where I have examined a specimen.

Young (50 mm. or less in length) are surprisingly rare. The only specimen I have previously had to examine (22 mm. long) was taken among weed in the Gulf Stream off Bimini in July with numerous *C. ruber* (Amer. Mus. Novitates, 1938, No. 1014, p. 1, fig. 1). It is then of much interest to obtain this series in late August from further northeast in the Stream, which is evidently a nursery ground for the species, very likely the important nursery ground for it in the western Atlantic. The majority are of such a small size at this point that they must be drifted far to the east before they reach a stage to navigate independently of currents, and so far as we know this is a littoral rather than pelagic fish when grown. An hypothesis that there is regular interchange between the continents of America and Africa, eastward in the north and westward in the south, should be investigated.

It may be more than coincidence that *crysos* and *ruber*, our two species with young most confined to the Stream, grow into the slenderest, swiftest, and presumably individually widest ranging. If it is temperature that holds the young of *crysos* in the Stream, as has been suggested for *ruber*, they must be more sensitive to it than grown fish, for grown *crysos* enters temperate waters more freely than any other except *hippos*. If there is a food habit factor of which gill-rakers may be a criterion, those of *ruber* are the finest and most numerous, but *crysos*, though more related to *sexfasciatus* and *hippos*, with few gill-rakers, has the next most numerous, more than *bartholomaei* which is closely related to *ruber*.

Descriptive Notes

Proportional changes with growth in *Caranx crysos* over 100 mm. standard length have recently been published (Amer. Mus. Novitates, 1938, No. 1014, pp. 2–3), and one can now complete them, for smaller sizes. Fourteen specimens 12 to 19 mm. in standard length have depth in same 2 to 2.2 (average 2.08); head, 2.4 to 3 (2.69); eye in head, 2.5 to 3 (2.67); pectoral 1.4 to 1.8 (1.59); curve lateral line (chord) in straight part, 1.5 to 1.6 (1.57). Sixteen specimens of 20 to 26 mm. have depth 2.2 to 2.6 (average 2.38); head, 2.7 to 3.2 (2.96); eye, 2.7 to 3 (2.96); pectoral, 1.4 to 1.6 (1.46); curve lateral line in straight part, 1.5 to 1.8 (1.62); about 30 to 34 (average 31.1) scutes may be counted. Five specimens of 28 to 30 mm. have depth 2.5 to 2.7 (average 2.56); head, 3 to 3.2 (3.04); eye 3 to 3.3 (3.06); pectoral, 1.5 (1.5); curve lat. line in straight part, 1.6 to 1.8 (1.72); 32 to 38 (35.2½) scutes may be counted. Eight specimens of 31 to 40 mm. have depth 2.6 to 3 (average 2.76); head, 3 to 3.4 (3.17½); eye, 3 to 3.5 (3.29); pectoral, 1.3 to 1.5 (1.45); curve lat. line in straight part, 1.6 to 1.8 (1.65); 33 to 38 (36.1) scutes may be counted. Three specimens of 42 to 48 mm. have depth 2.7 to 2.8 (2.77); head 3.2 to 3.3 (3.27); eye, 3.3 to 3.5 (3.43); pectoral 1.4 (1.4); curve lat. line in straight part, 1.6½ to 1.7½ (1.70); 30 to 41

(34.7) scutes may be counted. The one larger specimen of 72 mm. has depth, 3; head, 3.4; eye, 3.5; pectoral, 1.2½; curve of lat. line in straight part, 1.7; scutes, 47. Of almost exactly the same depth below 20 mm., and at larger sizes, their depth falls off more rapidly than that of *ruber* and they are more slender than that species between 30 and 40 mm.

Small young of *Caranx crysos*, down to the smallest sizes in this series, may be recognized by the character of the pigment spots on the body, some of which are larger and more conspicuous than in other members of the genus at comparable sizes (Amer. Mus. Novitates, 1938, No. 1014, fig. 1). Some of the specimens are paler, some darker, but aside from these punctulations few show traces remaining of any pattern; one of 18 mm. has 6 dark bands on the sides separated by narrower interspaces; two or three of from 20 to 26 mm. have about 7 or 8 faint dark crossbands on the body; and one of 48 mm. a dark edge to the corner of the gill-cover. The relatively long straight part of the lateral line will differentiate *crysos*, except from *sexfasciatus*, which is deeper with bolder cross-bands. Other species have punctulations not differing in kind from those of *crysos* but usually less heavy, less variable in size (none so large), and less conspicuous.

CARANX SEXFASCIATUS Quoy and Gaimard

There is one specimen 25 mm. in standard length from 21° 43′ 20″ N., 72° 39′ 15″ W., April 7 (Pawnee, 1927, 500 to 1000 ft. wire); 2 specimens of 12 and 15 mm., with 16 *crysos*, from 36° 48′ N., 68° 55′ W. to 38° 59′ N., 69° 46′ W., August 27 to 28 (Atlantis, 1934, in sargassum).

Distribution

This is a circumtropical species in warm seas, with several poorly defined races. These specimens presumably belong to the West Indian race, *Caranx sexfasciatus fallax* Cuvier and Valenciennes, but another occurs on the coast of Brazil (Rio de Janeiro, Amer. Mus. Novitates, 1938, No. 998, p. 2).

Grown *Caranx sexfasciatus fallax* occur, but in small numbers, from southern Florida to North Carolina, and are rare or absent further north. They are plentiful in the Bahamas and in Haiti, common about Cuba, and the most abundant member of the genus in Porto Rico and Bermuda.

I have examined a few scattered young of 40 to 50 mm. standard length from North and South Carolina and Havana, of less than 70 mm. from Porto Rico, but have no knowledge of where they are common, or what their proper habitat may be. These three specimens are the smallest I have seen.

Descriptive Notes

For comparison with somewhat larger specimens (Amer. Mus. Novitates, 1937, No. 967, pp. 3–4) the two 12 and 15 mm. in standard length have depth, 1.6 to 1.9 (average 1.75); head, about 2.6; eye, about 2.5; pectoral, 1.5 to 1.6 (average 1.55); curve of lateral line in straight part, 1.3½ to 1.4 (average 1.37½). The 25 mm. specimen has depth, 1.9; head, 2.7; eye, 3.1; pectoral, 1.5; curve of lateral line in straight part, 1.5½; and about 21 scutes may be counted. The three have 4 to 5 broad dark cross bands on the body, the larger specimen a less distinct slanting dark band from nape to eye, and the spinous dorsal largely blackish.

CARANX HIPPOS (Linnaeus)

There is only one specimen of this species, 13 mm. in standard length, Feb. 15 (Atlantis, 1934).

Distribution

Grown fish are plentiful along shore from southern Florida to the Carolinas, and the most common species in summer north to Cape Cod, small sizes entering estuaries rather freely. They are common about Cuba, fairly common about Haiti, not common about Porto Rico and in the Bahamas, apparently unknown at Bermuda. Specimens from Brazil and West Africa seem to be racially differentiable from those of the United States and West Indies.

Young are rather common occurring scatteringly near shore from Florida to South Carolina, and northward to Cape Cod in late summer and fall. We have one from gulf-weed off Bimini, and they doubtless not infrequently occur in weed, though under jellyfish is probably a more usual hover for them. They become free swimming in shallow water at a small size. The practical absence of young *hippos* in this collection confirms their littoral rather than off-shore habitat.

Descriptive Notes

As the one specimen is somewhat smaller than those previously reported on (Amer. Mus. Novitates, 1937, No. 967, pp. 1–3), its proportional measurements are given. Standard length, 13 mm.; depth in this length, 1.6½; head, 2.8; eye in head, 3; pectoral, 1.6; curve of lateral line (chord), in straight part, 1. Five broad dark bands crossing upper part of body, somewhat broader than the interspaces, another to the upper angle of the opercle, and a slanting band from nape to eye; spinous dorsal mostly blackish.

SUMMARY AND CONCLUSIONS

(1) The Gulf Stream is confirmed as a nursery ground for *Caranx ruber*, from May to August. In April young of this species averaging a little more advanced, are also found in the Windward Passage south of Guantanamo Bay, and plentifully in the Caribbean between Misteriosa Bank and Yucatan.

(2) Study of the considerable series of young *Caranx ruber* shows that this species is appreciably though but little more slender than *C. bartholomaei* at the

smaller sizes, with a slight overlap in depth between the critical lengths of 20 and 30 mm. standard, presumably due to variation in each, of the size at which depth falls off.

(3) The absence of young *Caranx bartholomaei*, most specialized for drifting in gulf-weed, from Gulf Stream localities, is evidence that its nursery grounds are not in the current but in comparatively dead water at or beyond the edges of same.

(4) A nursery ground for *Caranx crysos* for which none was previously known, is discovered in the Gulf Stream between latitudes 37° 12′ and 38° 59′ N., longitudes 67° 39′ and 69° 46′ W., in late August.

(5) The presence of young *Caranx crysos* so far to the northeast at a small average size suggests the possibility that this species may drift to the west coast of Africa where it also occurs. The rarity of young *C. crysos* and *C. ruber*, with nursery grounds in the Gulf Stream, along the coast of the United States, is discussed but not explained.

(6) This first good series of young *Caranx crysos* of less than 50 mm. standard length to be studied, confirms the character of pigment spots, of which some are scatteringly large and conspicuous, as one to distinguish this species from its relatives at small sizes. Another good character is the relatively long straight part of the lateral line. The depth of *Caranx crysos* is the same as that of *Caranx ruber* at less than 20 mm., but then falls off more rapidly and it is a somewhat slenderer fish at between 30 and 40 mm.

(7) The few specimens of *Caranx sexfasciatus* add nothing to our scant knowledge of the habits and habitat of its young; and that but a single specimen represents *Caranx hippos* confirms its nursery grounds to be inshore rather than off-shore. The somewhat smaller size of these specimens of the two than of those previously examined, makes them of some interest.

(8) Young caranxes of from 15 to 40 mm. in standard length, look quite unlike the adults, and their specific characters of fin-rays, gill-rakers, scales, can frequently not be determined with precision, or without difficulty. The following key which can now be drawn up for the five under discussion, will give an idea of their resemblances and differences, and be helpful in distinguishing them or identifying any individual.

Key to young Caranx of West Indian Region

1 Deeper, depth in standard length less than 2.0 .... see *2*

Moderately deep, depth in standard length 2.0 to 2.6 .... see *5*

More slender, depth in standard length, 2.7 or more .... see *4*

2 Body usually without bands, curve of lateral line about equal to straight part; dorsal soft rays, 24 to 28; anal, 22 to 25; ventrals often dusky and sometimes pale blotches on the body .... *bartholomaei*

Body with about 5 dark cross-bands. Dorsal soft rays, 18 to 21; anal, 16 to 18. Ventrals not dusky, and never pale blotches on the body.... see *3*

3 Curve of lateral line in straight part, 1 to 1.3 .... *hippos*

Curve of lateral line in straight part, 1.3½ to 1.6 .... *sexfasciatus*

4 Curve of lateral line in straight part, 1 to 1.3 .... *ruber*

Curve of lateral line in straight part, 1.5 to 1.8 .... *crysos*

5 Curve of lateral line in straight part, 1.5 to 1.8; about 30 to 40 scutes may be counted at 20 to 40 mm.; body usually without bands, when these are present they are more than 5 and usually indistinct, pigment spots relatively conspicuous, some relatively large and scattered; depth in length 2.4 and upwards at 25 mm. and upwards .... *crysos*

Curve of lateral line in straight part, 1.35 to 1.6; about 20 to 30 scutes may be counted at 20 to 40 mm.; body with about 5 distinct dark bands; depth 2 (or less) to 2.5 between 25 and 40 mm.................... *sexfasciatus*

Curve of lateral line in straight part, 1.3 or less .... see *6*

6 Body with about 5 (usually bold) dark crossbands; dorsal soft rays, 18 to 21; anal, 16 to 18; ventrals not dusky, and never pale blotches on the body. .... *hippos*

Body without or with indistinct crossbands, dorsal soft rays, 24 to 28; anal, 22 to 25... see *7*

7 Depth in length, not more than 2.3, 2.1 or less at under 26 mm.; not more than 20 gill rakers on the lower limb of the first arch; ventrals frequently dusky, and sometimes pale blotches on the body .... *bartholomaei*

Depth in length, upwards of 2.4 at over 30 mm.; upwards of 25 gill-rakers on the lower limb of the first arch; ventrals rarely slightly dusky, never pale blotches on the body .... *ruber*

Contribution No. 234

Vol. VI, Art. 7.

QUANTITATIVE OBSERVATIONS ON THE PELAGIC SARGASSUM VEGETATION OF THE WESTERN NORTH ATLANTIC

WITH PRELIMINARY DISCUSSION OF MORPHOLOGY AND RELATIONSHIPS[1]

BY ALBERT EIDE PARR

Bingham Oceanographic Laboratory

CONTENTS

Page
INTRODUCTION 2
METHOD 4
VERTICAL DISPERSAL OF FLOATING WEEDS 8
TAXONOMIC DISCUSSION 11
  ARTIFICIAL KEY TO DRIFTING WEEDS 15
  ECOLOGICAL CLASSIFICATION 22
  DESCRIPTIVE ATLAS OF EUPELAGIC WEEDS 23
    S. natans series 26
    S. fluitans series 36
  PRELIMINARY DISCUSSION OF RELATIONSHIPS OF EUPELAGIC WEEDS 46
    Description of fertile, attached plant of *S. fluitans* 49
GENERAL QUANTITATIVE AND GEOGRAPHICAL RESULTS 51
  DOMINANT FORMS (*S. natans* I and *S. fluitans*) 52
    Caribbean and Cayman Seas 53
    Gulf of Mexico 54
    Sargasso Sea 58
      Annual fluctuations 63
      Correlated variations in weed distribution 65
  DISTRIBUTION OF LESS ABUNDANT FORMS 65
  TOTAL QUANTITY OF PELAGIC VEGETATION 67
DURATION AND NATURE OF PELAGIC PHASE OF THE FLOATING SARGASSA 68
LIST OF HAULS 85
SUMMARY 90

---

[1] Joint contribution from Woods Hole Oceanographic Institution (No. 234) and Bingham Oceanographic Foundation.

INTRODUCTION

Since the days of Columbus, the enormous amounts of floating weeds drifting about in the so-called Sargasso Sea have excited the interest of scientists and of laymen as well; and in laymen's minds the most exaggerated myths have grown around the phenomenon, not always without scientific pretense. Since the earlier investigations and theories have already been fully reviewed by Krümmel (1891) and by Winge (1923), it will not be necessary in this report to give any detailed account of the past history of the sargasso weed problems in the scientific literature. Suffice it to say that in spite of the widespread interest most of the earlier studies have been largely speculative and purely incidental, apart only from the investigations of Krümmel, of Antze, his successor in this work, and of Winge. In the works of Krümmel and Winge, we see the first two organized attempts at a semi-quantitative approach along widely different lines. In both cases, however, the quantitative aspect was only arrived at by deduction from, and statistical treatment of, data which were not in themselves truly representative in a quantitative sense.

The basis for Krümmel's investigations was provided by the records of floating weeds observed from German ships crossing the North Atlantic and entered in their log-books as required by the "Deutsche Seewarte" over a period of many years. From these data the frequency of observation per geographical coordinate unit (1° square)[1] were calculated and plotted to show the boundaries of the Sargasso Sea, and its subdivisions into more or less concentric regions of various degrees of frequency of the floating weeds. Although of very great interest and value, the figures thus obtained obviously remain only purely numerical with no indication of their quantitative significance in terms of weights or volumes (see page 70).

Winge's material, on the other hand, was of an entirely different kind, consisting of the actual samples collected by various Danish research and merchant ships. These samples obtained a semi-quantitative significance from the fact that they were not dipped up separately but were brought in as part of the material collected in plankton-net hauls near the surface. Since, however, it is not feasible to estimate the surface area taken in by such a tow, with a circular net which does not operate strictly and uniformly at the surface, it would be

---

[2] Not, of course, a true unit of area except for squares in identical latitude.

quite impossible to try to convert the values obtained from such samples into quantitative figures per unit area even if the log distances of the hauls were known (this is not mentioned by Winge, who merely states their usual duration to have been about half an hour). Nor is any such attempt made by Winge, who confines his presentation of the semi-quantitative aspects of his material to indications of the size of the samples by the size of the dots by which they are represented on his distribution chart (Winge, 1923, fig. 22, p. 14) without any numerical tabulations or citations in the text. The quantitative significance of Winge's material is thus purely relative, with no suggestion of absolute values. It may further be stated on the basis of the experience gained during the present investigation, that even the extensive series of samples studied by Winge, which was undoubtedly by far the largest material purposely collected for a special investigation up to that time, can hardly have been adequate to give a reliable picture even of relative distributions and abundances.[1] Winge accordingly very properly confines his treatment of gross distribution to a mere fixation of the outer boundary for the regular occurrence of the typical drifting weeds, that is generally speaking simply the boundary between their presence in any amounts at all, and their absolute absence under normal circumstances.

In connection with a series of hydrographic cruises to the Central American Seas on the research ship "Atlantis," sponsored jointly by the Woods Hole Oceanographic Institution and by Yale University (under the auspices of the Bingham Oceanographic Foundation) an opportunity offered to carry further the work of Krümmel, Antze, and Winge in the western portion of the Sargasso Sea, and to attempt to put the problems on an absolute quantitative basis. For this purpose a very simple surface scoop-net, to be towed by the ship while under way between stations, was designed especially for the collecting of drifting weeds. In the course of the work so far this net has been in

[1] Winge's chart (loc. cit. fig. 2) shows a total of 185 samples (positive hauls) and 209 negative hauls for the entire North Atlantic over a period of 12 years (1911–1922), of which 173 positive and 44 negative hauls fall within the boundary of the about 8 million square kilometers of the Sargasso Sea as indicated by Winge. With the extremely unequal distribution of the weeds even in the regions of their greatest abundance, and with the very important annual fluctuations in the total amounts present, observed in the course of the investigation here reported upon, the wisdom of Winge's commendable restraint in the quantitative treatment of his material is obvious.

actual operation in the surface of the sea over a cumulative distance of seven thousand (6998) nautical miles, with a total of nearly five thousand (4759) pounds of pelagic weeds brought on board for sorting and weighing. It is the data and material thus gathered which form the basis of this first, and in various respects preliminary, report on these *Sargassum* investigations.

In the present paper we are exclusively concerned with the plants themselves, chiefly with their quantitative distribution only, and with the conclusions which the quantitative data may enable us to draw with regard to the question of maintenance of the pelagic vegetation.

To establish the necessary definitions, the weeds themselves will be described and illustrated in considerable detail, but their taxonomy can only be dealt with in a purely tentative manner. The problems of the ecology of the animal life associated with the *Sargassum* weed flora will be reported upon separately by M. D. Burkenroad and will not be considered in this paper.

METHOD

The collector shown in the accompanying figure 1 was towed at the normal cruising speed of the ship from the head of the hydrographic boom, which was kept swung out over the side so as to bring the net beyond the disturbing influences in the wake of the hull itself. The distortion of the quantitative results which might arise from the artificial concentration of weeds immediately along the side of the ship, where the surface water is being displaced by its passage, was thus avoided. It was, on the other hand, not practicable to bring the collector beyond the influence of the rapidly spreading bow wave under the conditions of work on board.[1] There was no observable indication, however, that the bow wave might have any appreciable effect upon the *amount* of weeds entering the collector, except possibly in very rough weather. While the bow wave will, of course, change the position of individual plants to a slight extent, so that other specimens may reach the net than those which would have been caught in the absence of the wave, the bow wave did not, away from the immediate path of the hull itself, cause any noticeable change in the *density* of weed distribution and therefore not in the *quantity* but only in the identity of the individual plants obtained in the collector. Significant changes in the density of weeds seem entirely limited to the wake of the ship and its immediate boundaries on the two sides, which were avoided. The author is therefore confident that the net has normally been so placed as to obtain a truly representative catch, within the limits of its efficiency (see below), at least in a sufficiently close approximation for all purposes of this investigation.

---

[1] This might also be easily accomplished by a simple arrangement on the otter-board principle; but would entail more labor than the other purposes of these cruises would permit.

It has been found that the net can be operated successfully under favorable conditions at cruising speeds up to 10 knots, but in a rough sea 7–8 knots would seem to be the maximum. The length of the towing wire must, of course, be so adjusted as to keep the upper horizontal bar of the collector opening above surface at all times. With a fairly high attachment of the wire, so that a relatively great length is required, this adjustment can be very easily accomplished and maintained even in quite rough weather. Low attachment with a short length is disadvantageous and makes the control difficult. With suitable adjustments and reasonably favorable conditions the collector hardly ever skips the surface, and only rarely submerges the top of its frame on a heavy roll of the ship. Skipping and diving, however, are the factors which limit the usability of the gear in rough weather, and under such circumstances collecting has always been abandoned until conditions have improved. Even when not skipping

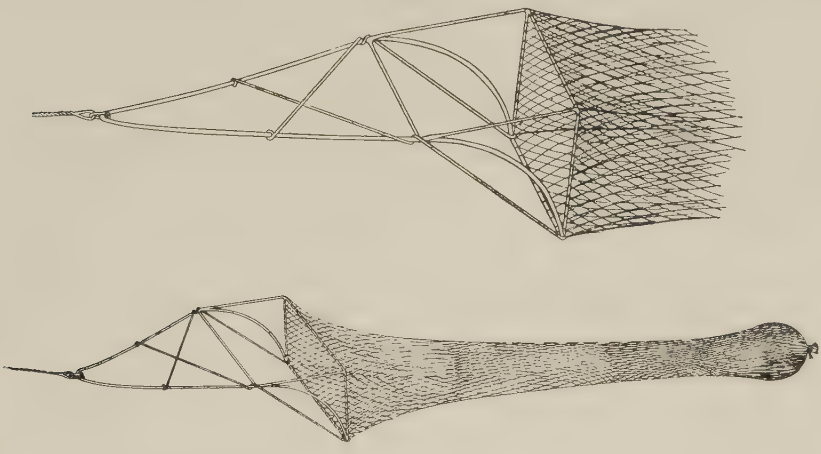


Figure 1. Pelagic weed collector. Detail of frame, *above* (see text); entire net, *below.*

and diving, the collector will, of course, not maintain an absolutely constant level in the sea and will occasionally rise high enough to permit some floating plants to escape below.[1] This, in the author's opinion, is the main and probably the only significant source of error in the approximative value of the quantitative results. While our figures therefore give only minimum values, innumerably repeated observations of the collector in operation[2] have convinced the author that this error can on the average probably not exceed 10 per cent, and is certainly less than 25 per cent of the true value, this error being, of course, entirely negative so that the recorded catches represent minimum values for the true abundance of the weeds.

The square metal frame for the opening of the net is exactly 2 feet wide inside and 20¼ inches high. The median length from the top horizontal cross-bar to the forward end of the bridle part of the framework is 5 feet. The main parts, i. e. the arched bridle irons and bottom cross-bar, were made of ⅝″ round steel, the braces and the remaining framework for the square opening of the net of ⅜″ steel.

The net itself is cylindrical, 11 feet long and of uniform width, 8 feet in circumference. The posterior end is simply closed and lashed tight with a short rope when the net is made ready for a haul. The first 3 feet have 1½ inch stretched mesh (¾″ square) of 18-thread medium twine; the following 3 feet 1 inch stretched mesh (½″ square) of 15-thread medium twine; and the last 5 feet ½ inch stretched mesh (¼″ square) of 6-thread medium twine.

It is important to have the forward bridle portion of the collector frame, by which it is attached to the wire, curve slightly upward as shown in our figure as it was found experimentally that this is necessary to keep the collector from turning over too easily. With the proper curvature its position in the water is very stable, and it is only rarely upset by a wave.

It was found very convenient to have the collector attached both to the hydrographic wire, letting this remain slack while towing, and to a heavier towing wire which carries the strain while the net is in the water, the hydrographic winch and wire being used only for lifting and setting the gear (without reducing the ship's speed), for which its strength is more than adequate.

---

[1] Deepening the opening would probably not remove this factor, since the collector rises to reach an equilibrium between the oblique strain due to its friction in the water and the vertical gravitational forces, and would therefore only rise higher to reduce the strain to the same point. Weighting of the frame would patently be disadvantageous under normal conditions (causing shortening of wire and increased tendency to dive).

[2] Since the collector is usually parallel with the stern of the ship, it can be easily and directly observed from deck.

The duration of each haul was made dependent upon the ship's and the staff's convenience, except when weeds were very abundant, in which case the collector must always be lifted as soon as the load in the net reaches a reasonable size, which can easily be judged by observations from the deck of the ship. The length of each haul has been determined by recording the reading of the ship's log at the beginning and at the end. This also gives a very convenient method of determining its geographical location by reference to the log reading at the noon position of the ship.

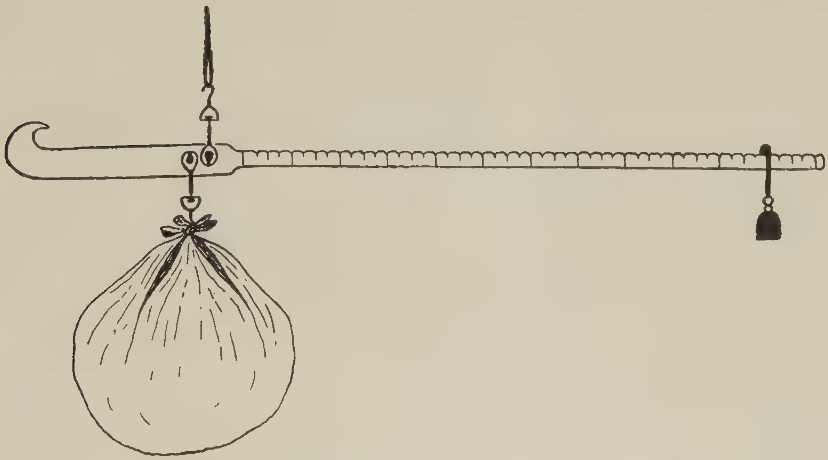


Figure 2. **Scales used for weighing weeds on shipboard.**

After the haul has been sorted the various species of weeds have been weighed separately in a fresh condition (wet, not desiccated) in cheesecloth bundles of suitable size by the use of an old-fashioned beam scale with a movable weight, swinging free from a strap above, as indicated in the accompanying diagram. It may be worth mentioning from practical experience that this type of beam scale would seem to be the only equipment fully suitable for such weighings on shipboard. Spring scales of any type are impractical at sea for the obvious reason that they will reflect the rise and fall of the ship in a bobbing up and down of their readings and of the object to be weighed. This difficulty is avoided in scales working on the principle of equal momentums balanced against each other, since both sides are then affected in the same manner by the movements of the ship, but it is further necessary also to avoid even beam scales which do not swing free in all directions so that no frictional or momentum differences may develop by an inclination of the instrument in accordance with the varying inclinations of the ship. The simplest equipment to fulfill these requirements is undoubtedly the instrument here used.

Weights have been read to nearest ¼ pound. Total hauls less than one pound of all species combined, or less than ¼ pound of a single species have merely been recorded by the presence of the various forms of *Sargassum* found therein.

After weighing, generous samples of all varieties present have been preserved in cheesecloth bundles kept in 10 per cent neutralized formalin in 30–50 gallon oak barrels. Samples of these samples have subsequently been pressed and mounted on herbarium sheets in the Bingham Laboratory. As a practical suggestion, perhaps already familiar to the botanists, one might mention that it has been found advantageous in the case of stiff and recalcitrant specimens first to put them under press between blotters for 12–24 hours, and thereafter soak them again in water, after which treatment they readily yield to the desired arrangement of leaves and branches. No thinning out of the specimens has been undertaken in preparing them for the herbarium, since the total habitus of the plant is an important feature in investigations of the kind here undertaken.

VERTICAL DISPERSAL OF FLOATING WEEDS

One may sometimes hear or see the statement made by travelers that they have observed pelagic weeds drifting by quite deep down in the water. Apart from occurrences in the turmoil of the wake or in the leeway of a ship, these assertions are quite contrary to the author's own experience in so far as any at all quantitatively significant frequency is concerned. It is also contrary to mechanical probability that the weeds should be able to drift at any significant distance below the surface for a sufficient length of time to produce a vertical dispersal of sufficient importance to require consideration in a quantitative investigation, for the reason that when a weed becomes accidentally submerged it will rapidly be losing buoyancy by compression of the gases in its bladders, and if it gets beyond the point at which it will continue to sink indefinitely its further descent will for this reason be an accelerated movement.[1] Inversely, the ascent of plants which have not reached the sinking point will also be an accelerated movement due to the expansion of their bladders as the pressure is again reduced. This will also hold true even if the plants should have a certain ability to regulate the gas contents of their bladders according to requirements (this is a point well worth investigating), unless their power of regulation should be able to function with great rapidity, which seems extremely unlikely in any case. With both ascent and descent from a submerged level thus being accelerated motions, the likelihood of a plant accidentally maintaining equilibrium for any length of time at a subsurface level is, or course, extremely slight; the more so since it is normally only likely to become submerged under conditions of great turbulence.

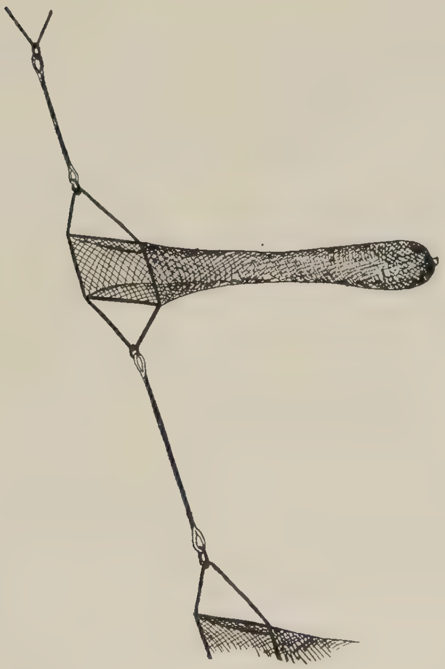


Figure 3. Collecting net frames used for study of vertical dispersal. Note that wire crossing opening of nets to block entrance of weeds has been avoided.

To substantiate by direct evidence our assumption that pelagic weeds under normal conditions occur in quantitatively significant amounts only at the very surface itself, a 24.3 mile haul (No. 151) was made with 5 nets suspended below each other along the same wire, using a different type of frame as illustrated in our figure 3. The results were the following:

---

[1] It is not impossible that violent storms may cause a certain loss of entire plants by forcing them down below the sinking point through mechanical turbulence, although this loss will probably be slight.

Net 1. Normal position at surface, but with more diving than usual, due to less favorable wire angle required for the operation of the entire set. Quantities therefore minimum values:

37.5 lb.	*S. natans I* (1.54 lb. per mile)
9.0 "	*S. fluitans III* (0. 37 lb. per mile)
4.0 "	*S. fluitans X* (0.17 lb. per mile)
1.5 "	*S. natans II* (0.06 lb. per mile)
52.0 lb.	Total Weeds

Net. 2. Top horizontal bar averaging about 1.5 meters vertical depth. Catching at surface while net No. 1 was being attached (unavoidable).

0.45 lb. Total Weeds. Probably mostly caught at surface.

Net 3. Top horizontal bar averaging avout 5–6 meters vertical depth. A couple of plants observed entering at surface.

2 small plants (taken at surface).

Net 4. Top horizontal bar averaging about 15–18 meters vertical depth. One small plant observed entering at surface.

1 small plant (taken at surface).

Net 5. Top horizontal bar averaging about 35–40 meters vertical depth.

Empty.

In other words, not even No. 2 net, operating only 1.5 meters below the surface, gave a quantitatively significant catch in proportion to the catch made at the surface, the weeds actually collected at the depth at which No. 2 net was intended to operate weighing less than 1/100 of the total weight of weeds obtained in the surface net. Furthermore, nothing was obtained in any of the deeper nets from their proper level. In quantitative investigations of the floating *Sargassum* vegetation collecting at the surface alone will therefore give an adequate picture of abundance in absolute terms with only the reservations already made on page 6.

TAXONOMIC DISCUSSION

An inspection of the available literature on the genus *Sargassum* cannot fail to impress one very strongly with the prevailing state of uncertainty in regard to the classification and nomenclature of many, if not most, of its members in the western Atlantic. In any given area it generally seems fairly easy to differentiate the local *Sargassum* flora into a comparatively few (say 2–5) locally distinct benthonic forms, plus the usual two pelagic "species" found drifted ashore. But in a comparison between descriptions or material from different regions it frequently becomes very difficult to speak with any assurance of absolute taxonomic identities or distinctions. Compared over their entire range of distribution many of the forms show a distressing tendency towards more or less complete intergradations and the question arises as to whether these intergradations are real or apparent, that is whether they are the result of parallel modifications of phylogenetically distinct strains, or actually express a systematic continuity through local variations.

Unquestionably the genus *Sargassum* thus offers great inherent obstacles to a clear understanding of its taxonomy, and different possibilities suggest themselves in explanation of this situation. It is possible that the genus may comprise a great number of actually independent taxonomic units covering, in the aggregate, a very wide range of morphological differences, but being so closely intergraded within this range as to defy clear definition and reliable recognition of each unit separately. It is also possible that there may in reality be only a very few truly independent forms of such great morphological instability under varying environmental conditions that the thread of their taxonomic affinities is very hard to follow through the maze of their phenotypic diversities. It may finally also be that we have a few quite stable and well differentiated forms combined with other systematic units of extreme morphological instability which serve to obscure the nomenclature and classification of the entire genus. In the author's opinion, the latter possibility is most likely to offer the true explanation of the inherent difficulties of *Sargassum* taxonomy. From the material so far studied it would for instance appear as though *Sargassum hystrix* might safely be regarded as a relatively quite stable form not subject to significant local modifications of its essential specific characteristics. This is apparently also true in a lesser degree of *S. polyceratium* and *S. platycarpum*. On the other hand, there can be no question of the great individual as well as geographical variability within the *S. vulgare*—*S. pteropleuron* group.

While the preceding remarks are applicable both to the benthonic and to the pelagic weeds, the classification of the latter offers further special difficulties of its own, arising from the fact that it has not as yet proved possible to establish definite specific affinities between the pelagic weeds and the sessile relatives from which they must be, or have been, derived. The question of whether the derivation of the floating forms is entirely a matter of past evolution or whether it also continues actively today, and whether the pelagic weeds should accordingly be dealt with as independent systematic (genotypic) units or merely as phenotypic variations of sessile species, directly induced by the changed conditions of the drifting stage, is therefore still unanswered. So long as this state of affairs remained unaltered, it was patently impossible to establish a definitive classification and nomenclature for the pelagic forms. This has been very strongly felt by Winge in his resort to numerical designations instead of binominal nomenclature; and it is only through samples discovered in the material here reported upon that the difficulty has finally been overcome for the first time in the case of one of the dominant floating weeds, heretofore known only in the sterile pelagic form.

While material is being gathered for a collateral investigation of the taxonomy and classification also of the benthonic species of *Sargassum*, with a view to elucidating the probable derivation and relationships of the pelagic weeds, this phase of the work has not yet reached a stage where it is possible to draw any definite conclusions. Nor is it necessary for the purposes of the present report on the quantitative observations made to date to enter into a discussion of the sessile relatives of the drifting forms to which our figures exclusively pertain. We shall therefore in the following confine ourselves to the description and discussion of those weeds which in the course of these investigations have been found to form part of the pelagic *Sargassum* flora.

For a convenient instrument for the identification of the benthonic species of the Western Atlantic, the reader may be referred to Howe's brief synopsis of the Bahaman flora (Howe, 1920), which, when supplemented by Collins and Hervey's key and descriptions of the *Sargassa* of Bermuda (Collins and Hervey, 1918, pp. 80–84), has been found most useful for a preliminary orientation of the shore collections examined by the writer. More extensive descriptions, but unfortunately only of a more limited number of species may also be found in Börgesen (1914 a, b) and Taylor (1928). It is clear, however, that much of the nomenclature and classification used by these various authors must still be considered to be of a purely tentative character.

In regard to the pelagic weeds, the most useful and most comprehensive account available to date is that given in Winge's report (Winge, 1923, pp. 21–29), and it has been particularly fortunate in the field work connected with these investigations to be able to refer constantly to Winge's text and illustrations in the task of sorting on board nearly five thousand pounds of floating plants and of correlating the zoological with the botanical observations made in that connection.

In Winge's account, however, the nomenclatural problems have been left entirely as they were and the prevailing uncertainties are emphasized by a resort to simple numerical designations instead of a binominal terminology. The probable relations between the various floating forms, as indicated by their morphological similarities or distinctions, are likewise given only scant consideration.

Although the results of the present investigation are as yet far from having eliminated all the difficulties which have hampered the discussions of the pelagic weeds in the past, they nevertheless lead forward along three different lines towards a better understanding of the taxonomic problems of the floating *Sargassa*.

On one hand the existing information concerning the diversity of morphological forms observable in the pelagic state is confirmed, and is further increased by the discovery of an additional variety (*S. natans, IX*) in one of the series or "species," tending to be dominant within its own domain, and of a dimorphic condition in another "species," (neither of which is mentioned in Winge's descriptions of the floating weeds). On the other hand, the extensive collections now available clearly show by their intergradations that at least three of the varieties tentatively treated as equivalent units in Winge's report,[1] plus the additional variety above mentioned, arrange themselves quite naturally into a single series, which may thus be treated as a taxonomic unit, tentatively given the rank of a species, and to which a binominal designation (*Sargassum natans*) can therefore be applied with full recognition of its possibly composite systematic character.

---

[1] Winge (1923, p. 28) is of the opinion "that the 8 species enumerated by [him] are «good species»." Of these only 6 are here considered under separate species headings.

Finally, the discovery of a fertile specimen of the other one of the two dominant pelagic weeds (*S. fluitans*), attached to a small piece of driftwood, has served to show that the sterile and unattached pelagic form of this species at least is not morphologically modified from the fertile and sessile type of plant in so far as vegetative parts are concerned, the modifications being, in other words, entirely confined to the loss of fertility alone. While this discovery has no direct bearing upon the question of the average duration of the pelagic state, or in other words, the average age afloat of the specimens constituting the oceanic *Sargassum* flora, it does enable us from now on to make definite search for benthonic fields of a known type of sessile *Sargassum* weed from which the recruiting of the pelagic population of *S. fluitans* may still be going on today, with the knowledge that evolutionary modifications calling for an *a priori* assumption that this recruiting must be entirely a matter of past history are at least not involved in the case of this particular one of the two dominant members of the floating *Sargassum* flora.

Before proceeding further with the discussion of the variations, relationships and distributions of each of the various forms of floating *Sargassum* with which we are here concerned, it is perhaps best first to give a brief synopsis of the definitions on which we have based the identifications and nomenclature, or numerical designations, to be used in this report. In this synopsis we shall only include the pelagically important forms, that is the forms found only in a pelagic state and those of the normally benthonic varieties which are apparently capable of maintaining a pelagic existence, without obvious degeneration or essential morphological modification, for a sufficient length of time to become significant members of the oceanic *Sargassum* flora. The synopsis thus covers all forms of *Sargassum* observed in *open ocean* in the course of this investigation, which can safely be taken to mean all forms at all likely to be found afloat at least in the western half of the Sargasso Sea proper. Only near shore, in the neritic margins of the pelagic domain, will holo-benthonic forms not defined in this key be likely to occur adrift at the surface, and for the identification of such weeds reference has already been made to Howe's work on the Bahaman forms (Howe, 1920) and to the synopsis of the Bermudian species given by Collins and Hervey (1917). To avoid duplication and confusion, Winge's numerical designations have been retained whenever it has been found impossible or inadvisable as yet to replace them with a binominal nomenclature, and new numerical designations have been introduced in sequence with Winge's, regardless of the fact that the resulting numerical sequence is in most instances without any relation to the writer's views on the probable relationships of the forms so designated.

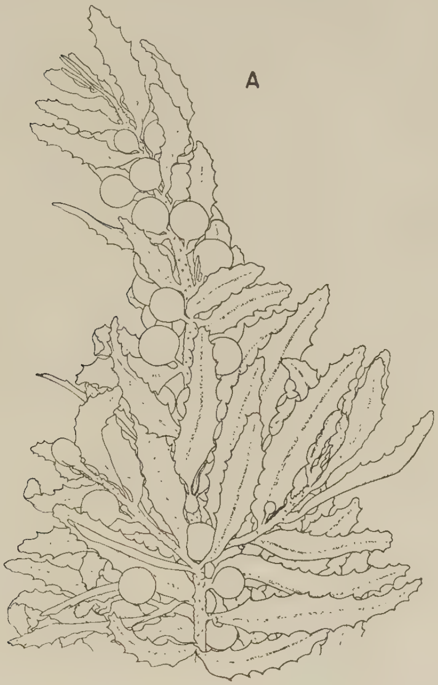


Figure 4. *Sargassum fluitans* (*X*). *A.* **Part of plant.** *B.* **Single branch. Drawn from formalin specimens by D. T. Pitcher. × 6/7.**

ARTIFICIAL KEY TO THE WEEDS FOUND IN PELAGIC COLLECTIONS

A. Dwarf form, size of plant usually only about 1 inch. Bladders small, very numerous. Stems thickly beset with long thorns. Leaves rare, very small when present. . . . . *Sargassum V*, Winge 1923.

B. Not dwarfed. Leaves present, usually abundant.

  I. Stems thorny, especially on distal parts.

    a. Leaves linguiform to ovate, usually flaccid when caught pelagically. Plants normally fertile, with receptacles (fruitleaves) present. Not a pelagic weed. . . . . . . *S. polyceratium* Montagne.
    ? *Sargassum IV* Winge, 1923.

b. Leaves lanceolate; edges dentate or serrate; midrib not very prominent, never winged or dentate. Always sterile, without receptacles.....................*S. fluitans* Börgesen 1914b.

1. Many subequal, close-set, short branches without distinct differentiation of main branches or stems. Entire plant typically of a dense, globular, or short cylindrical habitus. Branches of third and higher orders normally very short and obscured by the foliage. Foliation very dense, fully developed bladders usually greatly outnumbered by leaves. Leaves in fresh condition thicker and stiffer than in III. Color dark olive.................*S. fluitans* (*X*), Parr.
Basal shoot form of *S. fluitans*.
2. Usually only one or two long main branches, with relatively few, long, wide-set branches of the second and of higher orders, giving entire plant a loose, open and stringy habitus. Foliation less dense than in X. Fully-developed bladders usually more numerous than leaves.
S. fluitans (*III*).
Sargassum III, Winge 1923.
Distal shoot form of *S. fluitans*.

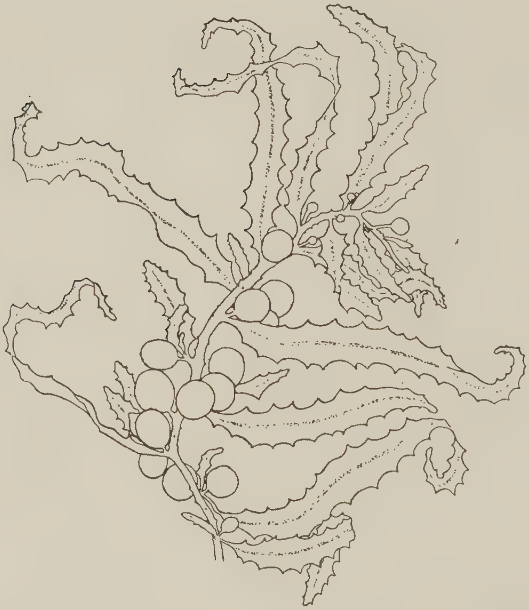


Figure 5. ***Sargassum fluitans* (*III*). Part of branch. Drawn from formalin specimen by D. T. Pitcher. × 6/7.**

c. Leaves linear to lanceolate. Plants normally fertile with receptacles present. Not pelagic weeds.
S. pteropleuron Grunow.
S. vulgare Agardh.

II. Stems smooth throughout.

a. Leaves thick, linguiform to ovate, bluntly rounded at their distal end, their margins subentire, entire or vaguely dentate. Habitus open and loose with very long and very wide-set branches of second order, with branches of third order generally *abruptly* smaller; or very dense, subcylindrical, with extremely short, profusely foliate branches of second order. Foliation always very dense, hiding the structural features of the entire plant, or at least on the distal portions of the secondary branches in the long-branched form. Color tending to dark tobacco-brown. Often fertile.....................*S. hystrix* Agardh.
? *Sargassum VI* Winge, 1923.[1]

b. Leaves thinner, narrowly to broadly lanceolate, or linguiform, always conspicuously dentate. Habitus always bushy, with generally *gradual* reduction in the size of the branches of higher order (not abrupt as in *S. hystrix*). Foliation always quite open and relatively sparse,[2] never obscuring the structural features of the plant. Color yellowish to brown. Never fertile.
S. natans Linneus, *sensu lato.*

1. Bladders with a shorter or longer spike at their distal end, sometimes developed into a narrow, leaf-like appendage. Leaves linear to narrowly lanceolate; when fully developed typically about 30–40 mm. long, .5–1 mm. wide, their width contained about 30–50 times in their length.[3] Habitus finer than in any of the following forms. *Average* distance between origins of branches[4] usually 6–8 mm., only rarely as little as 5 mm. Number of bladders actually

---

[1] In his key Winge (1923, p. 29) defines *Sargassum VI* as having stems without thorns, which agrees with *S. hystrix*, although Winge's illustration of *S. VI* (*loc. cit.* fig. 10, p. 25) otherwise shows rather more resemblance with our *S. fluitans X*.

[2] True also of *S. natans* (*IX*) in comparison with *S. hystrix*. *S. n.* (*IX*) can also be distinguished from *S. hystrix* by its narrowly lanceolate, strongly dentate leaves. Broad leaves in the *natans* series occur only in the very openly-growing (*VIII*).

[3] The broad-leaved variety, referred to *S. natans* (*I*) on the basis of the presence of bladder spikes, may have leaf-widths up to 3 mm., contained as little as 12 times only in their length.

[4] Excluding distal parts still actively growing.

present at any time usually only about half the number of leaves. . . . .*S. natans* (*I*).
Sargassum I, Winge 1923.
S. natans var. *ciliata* Börgesen 1914a.

2. Bladders quite smooth, without distal appendage of any sort.
    x. Very open growth. *Average* distance between origins of branches typically 7–8 mm., very rarely as little as 5 mm. Number of bladders actually present at any time usually considerably less than number of leaves.[1]
        o. Leaves (linear to) narrowly lanceolate, when fully developed typically about 40–60 mm. long and 1.5–3 mm. wide, their width con-

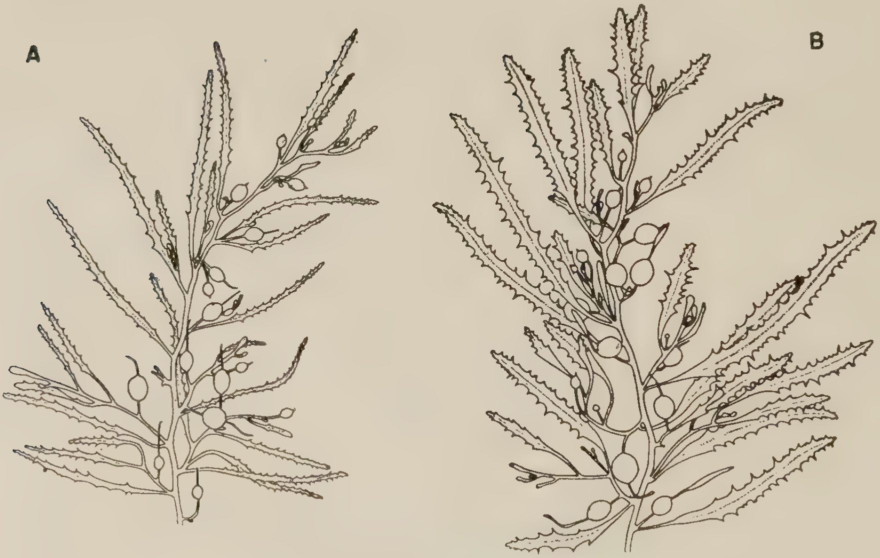


Figure 6. *Sargassum natans* (*I*). *A*. Narrow leaved. *B*. Broadleaved plant. Drawn from herbarium specimens by D. T. Pitcher. × 6/7.

---

[1] When counting the number of branches arising over a given distance from the stem under examination one must, of course, always be careful to exclude the apical portion in which the stem is still actively growing.

tained 15–30 times in their length. Habitus coarser and more open than in (*I*).

S. natans (*II*).
S. natans var. *typica* Börgesen 1914a.
Sargassum II, Winge 1923.

oo. Leaves lanceolate to broadly lanceolate, when fully developed typically about (25) 30–50 mm. long and 5–6 mm. wide, their width being contained about 5–10, typically 7–8 times in their length.[1] Habitus still coarser and more open than that of (*II*).

S. natans (*VIII*).
Sargassum VIII, Winge 1923.

xx. Denser growth. *Average* distance between origins of branches generally less than 5 mm. Number of bladders actually present at any time usually about equal to or greater than number of leaves. Leaves lanceolate, strongly dentate, when fully developed about 30–40 mm. long and 1.5–2.5 mm. wide, their width being contained about 15–25 times in their length.................... *S. natans* (*IX*), Parr.

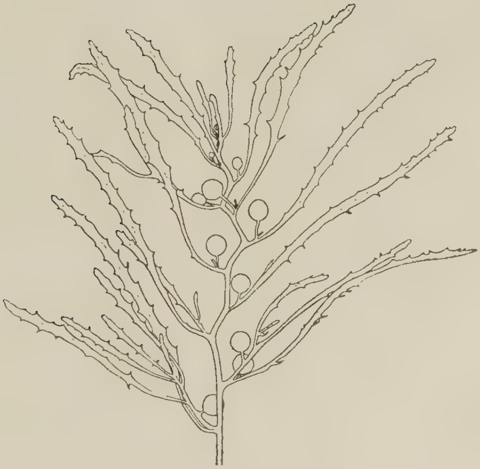


Figure 7. *Sargassum natans* (*II*). Drawn from herbarium specimen by D. T. Pitcher. × 6/7.

---

[1] In the typical floating form the absolute width of the leaf (ab. 5 mm.) is surprisingly constant regardless of variations in its length. Narrower leaves, of widths down to 2.5 mm. contained up to 15 times in their lengths, occur in atypical forms pointing in one form towards (*II*), in another form towards a benthonic origin.

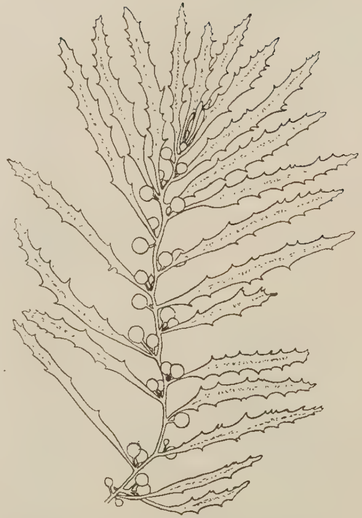


Figure 8. *Sargassum natans* (*IX*). Drawn from herbarium specimen by D. T. Pitcher. × 6/7.

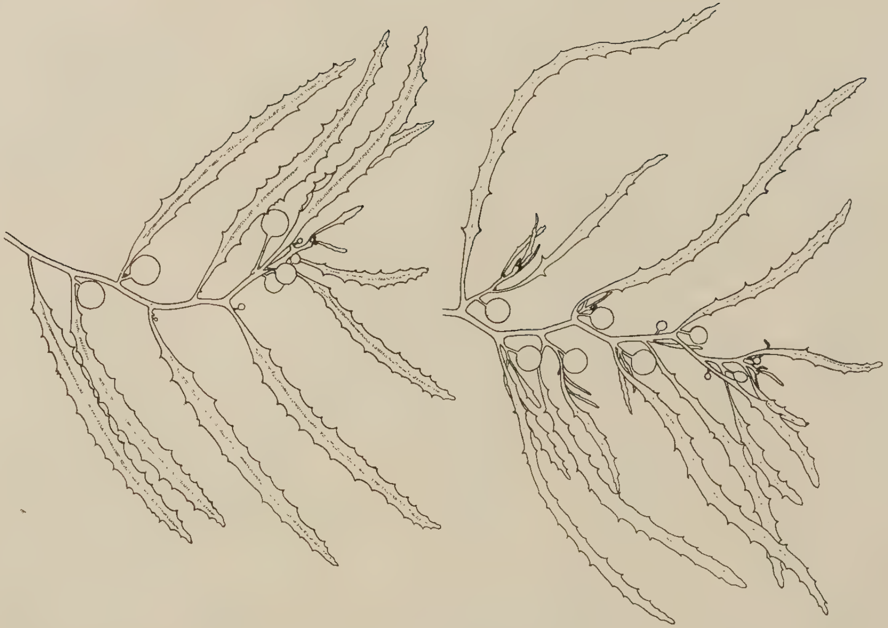


Figure 9. *Sargassum natans*. Transitions between (*II*) and (*VIII*). Drawn from herbarium specimens by D. T. Pitcher. × 6/7.

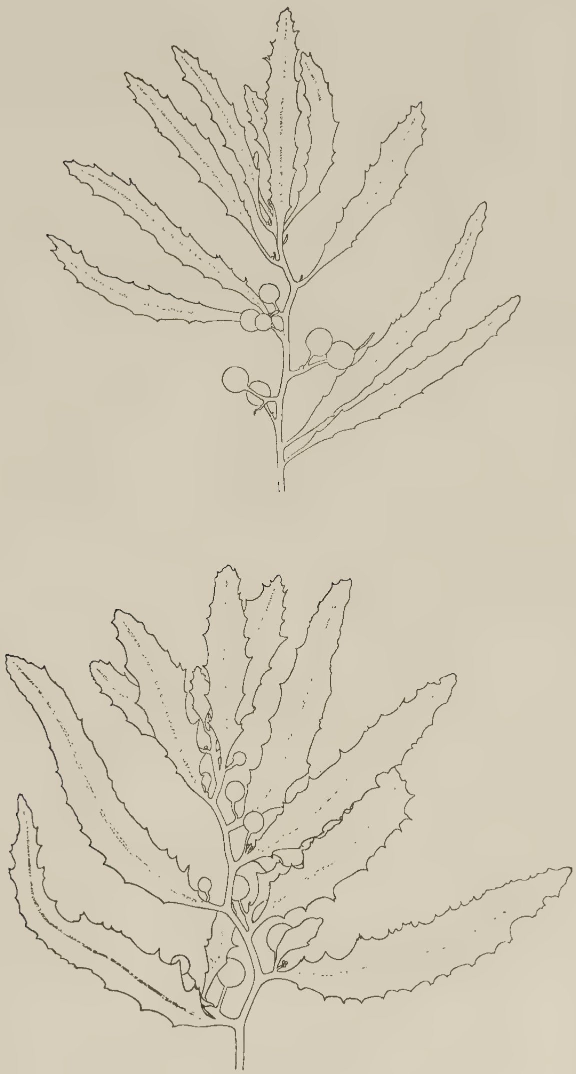


Figure 10. *Sargassum natans (VIII).* Branches of plants with medium and with broad leaves. Drawn from herbarium specimens by D. T. Pitcher. × 6/7.

ECOLOGICAL CLASSIFICATION

On an ecological basis, two or three different classes of floating weeds may be distinguished according to the roles they play in the pelagic flora and the role and duration of the pelagic stage in the ecology of the individual species. In one class we have the eupelagic weeds, that is the species or varieties of *Sargassum* which in a quantitative sense have their main occurrence in the pelagic condition or which are as yet only known at all in a floating stage. In this class we have the species or series of forms included under the designations of *S. natans* and *S. fluitans*. These eupelagic forms, of course, contribute by far the largest quantity of vegetation to the drifting community as were to be expected from their definition. In the second class, the quasipelagic forms, typically represented by *S. hystrix* and perhaps comprising no other form among those here considered, we might group the weeds which are normally benthonic and sessile, but which, when they are torn loose from the bottom, are able to survive in the pelagic condition, without significant morphological changes, for a sufficient length of time for them to contribute a quantitatively significant element to the floating flora in the peripheral parts of the Sargasso Sea without being able to maintain a significant representation in its central area, among the weeds of longer pelagic existence (see page 68). Finally, the third class may be made to comprise the holo-benthonic forms which are only accidentally found drifting at the surface, where they either rapidly perish (*S. polyceratium* and others) or rapidly become modified into a holopelagic form in which the identity with the benthonic type becomes unrecognizable (it is still not impossible that *S. natans* may be a derivation *with* morphological modifications from a benthonic form with which it can not as yet be identified). The forms of the holo-benthonic class are, of course, normally only encountered in the neritic boundaries of the Sargasso Sea proper, and it is only a very few of the holo-benthonic forms which have so far been found in pelagic collections at all, outside of the narrowest and most turbulent straits and coastal waters. Clearly the likelihood of finding a holo-benthonic form even accidentally present in a pelagic collection is determined (1) by the ease with which it is torn loose from its sessile condition which again will be dependent (a) upon the tensile strength of its stems, (b) upon the nature of the substratum generally selected for attachment (e. g., forms growing mainly on rocks and pilings are less likely to be found adrift than forms growing on smaller objects), and (c) upon the degree of exposure, generally correlated with depth, of their benthonic zone of distribution (the fact that *S. filipendula* seems so rare at the surface even in such a locality as the Straits of Florida is undoubtedly correlated with its generally relatively deep benthonic habitat in southern waters). It is further determined (2) by the degree and durability of the buoyancy of the weed when loosened. In the great amount of pelagic collections sorted in the course of this investigation only 3 holo-benthonic forms have been found to occur with sufficient frequency at the surface in the neritic margins to warrant their inclusion in our key on page 15.

While Winge does not explicitly classify the 8 varieties of floating weeds. described by him according to the relative importance of their pelagic as compared with their benthonic occurrence the implicit statements made in his text are quite in accordance with the grouping of the various "species" here suggested.

DESCRIPTIVE ATLAS OF EUPELAGIC WEEDS

The synopsis given in the preceding differentiates only the typical representatives of each of the various forms encountered in the course of these investigations. Actually, however, the eupelagic forms show every possible type of intergradation, even to intergradations (at least in superficial descriptive features) between the *S. fluitans* and *S. natans* series. It therefore seems desirable that the descriptive account of these variable and intergrading series should be further elaborated for future use in comparisons between collections. Since we are chiefly concerned with the eupelagic weeds only, we shall in the following confine our attention to the two series identified as *S. natans* and *S. fluitans*. In the hope that this may prove the most useful and practical method of presentation, the account will be given in the form of an annotated descriptive atlas of photographic herbarium silhouettes.

In this connection it should also be mentioned that the epizoan fauna inhabiting the weeds often provides valuable guidance for the classification of the weeds themselves, due to the specificity of certain dominant forms. The writer is indebted to M. D. Burkenroad for the following statement of these relationships and their probable interpretation.

> "Almost every individual plant of eupelagic *Sargassum* is overgrown by some one of a limited number of species of colonial epizoan which, upon the outer and younger portions of the plant at least, dominates the attached fauna. Each of these dominant species of epizoan is limited, not geographically or seasonally, but rather to certain forms of plant. Upon *S. I* of the *natans* series the dominant is almost without exception the sulphur-yellow Campanularian hydroid *Clytia noliformis*. Upon *S. natans II* the same *Clytia* is usually the dominant, and this hydroid occasionally occupies what appear to be plants of *S. VIII* and *S. IX* of the *natans* series. *S. natans IX* is, however, much more usually overgrown with the yellow Sertularian hydroid *Sertularia mayeri* or with the black species *S. flowersi*, which infrequently occupy what appears to be *S. II*. Upon *S. natans VIII* the dominant form is usually the white Plumularian hydroid *Aglaophenia minuta*. In the *fluitans* series, the usual dominant of *S. III* is the same species as in *S. natans VIII*, *Aglaophenia minuta;* on occasion, however, a plant of *S. fluitans III* may be overgrown by *Sertularia flowersi*, *S. mayeri*, the white branching *S. versluysi*, the white unbranched *S. brevicyathus*, the tan-colored Sertularian *Pasythea quadridentata*, or the delicate white Plumularian *Monotheca margaretta*. *S. X* of the *fluitans* series may have as its dominant hydroid *Clytia noliformis*, *Sertularia mayeri*, or *S. flowersi*, but frequently lacks a clear dominant; it is almost invariably occupied by a Chilostomatid bryozoan which never occurs upon any other form of holopelagic *Sargassum*. Finally, the dominant hydroid of *Sargassum V* is either of two species of Tubularian hydroid one of which resembles *Clava*, the other *Syncoryne*.
>
> A difference in hydroid fauna between broad-leaved and narrow-leaved forms of

pelagic *Sargassum* taken in the same locality was noted by Hentschel, 1920; and was remarked by Winge, 1923, as a supplement to the distinctions between *S. natans I* and *S. fluitans III*. The use of the faunal distinction for separation of intergradient or nearly resembling forms of *Sargassum*, as *S. natans II* and *S. natans VIII* or *IX*, *S. fluitans III* and *S. fluitans X*, is however complicated by the impossibility of determining whether a doubtful plant bears an unusual dominant, or whether it is an atypical plant with the usual dominant. Thus, typical *S. natans VIII* almost always bears *Aglaophenia*, and the plants occupied by *Clytia* or *Sertularia* are often of less characteristic form and might perhaps represent *S. natans II*. Further, according to what seems at present the most satisfactory hypothesis relative to the mechanics of distribution of the epizoa of pelagic *Sargassum*, the limitation of given epizoans to given forms of plant has more the quality of a succession phenomenon than that of, say, host-parasite specificity. Therefore, unusual combinations are to be expected, *especially upon plants of atypical form;* and the definition of boundaries between plant forms according to their epizoan associates would be an arbitrary procedure. The following facts and assumptions lead to the hypothesis in question:

In addition to the dominant colonial epizoans, each plant of pelagic *Sargassum* bears what may be termed a subfauna of hydroids (*Gemmaria*, *Halecium nanum*, *Plumularia setaceoides*, *P. catharina*, *Obelia*, *Clytia bicophora*, and others) and the very abundant bryozoan *Membranipora tuberculata* which (in sharp contrast to the dominant hydroids, more than one species of which is only infrequently found growing upon a single plant) may occur all together or in any combination, and in association with any dominant epizoan. The subfaunal epizoa, although more frequent upon some forms of *Sargassum* (*S. fluitans III*) than upon others (*S. natans I*), occur in much the same proportion one to another upon any form of plant. This nonspecific subfauna is most frequent, in contrast to the dominant epizoans, upon the older and inner parts of the plants; and its components often occur in small discrete patches, rather than as continuous extensive colonies. The subfauna is as a whole distinguished from the dominant forms by a much greater frequency of sexual reproduction or of the development of long transfer stolons.

The evidence seems irrefutable that floating *Sargassum* grows actively, that its older parts gradually break off and sink, and that its numerical abundance is maintained chiefly by division of the stock. It is therefore clear that a sterile dominant epizoan must keep pace with the extension of the plant upon which it grows, in order to avoid being lost with the older portions of the plant. On the other hand, the subfauna, reproducing sexually or with other special means of facilitating transfer from plant to plant, need not overgrow the entire plant to assure the maintenance of its stock; and its adjustment to the dynamic peculiarities of the substratum therefore need not be so close as in the case of the dominant epizoans.

Experiments made at the Bermuda Biological Station in 1936 suggest that the specificity and the exclusiveness of the dominant hydroids is not an immediate effect either of the substratum (successful transfers of *Aglaophenia* to *S. natans I*, etc.; ready growth of all forms on glass) or of the epizoan association (culture in mixed stands of the various dominant forms). Thus, for example, the limitation in nature of *Aglaophenia* to *S. fluitans III* and *S. natans VIII* is not a matter of direct and immediate dependence upon these specific plant substrata or of a directly deleterious effect of the tissue of *S. natans I;* and further, the lack in nature of any examples of *S. fluitans III* dominated by a mixture of *Aglaophenia* and *Pasythea* is not the result of a direct incompatability of one of these hydroids with the other. It therefore seems more likely that the apparent selectiveness exhibited by the dominant epizoans is the result either of a difference in the history of the plants or of some indirect, quantitative process, than that it is the result of a qualitative restriction.

Transfer of epizoans both dominant and subfaunal from one plant to another occurs without special means on the high sea to some extent, when the plants are massed together during protracted periods of calm, or are bound together by the silken tubes constructed by the nereid worm or by the amphipod *Sunamphithoë*, or by the egg-strands of flying-fishes. Such transfer seems to occur with sufficient, although a low, frequency to have produced a complete mixture of originally separate dominant faunas, given the long period of pelagic existence of the plants for which the evidence seems clear. It therefore appears that the assumption of an originally distinct geographical derivation of *S. natans I* and *S. fluitans III*, or of the plants of *S. fluitans III* with *Aglaophenia* from those with *Pasythea*, can not serve to account for the observed distinctions in dominant fauna.

The simplest explanation of the peculiarities of distribution of the dominant epizoans might in part at least be supplied by an assumed relation of their individual rates of growth to that of the different plants and of each other. *S. natans I* never bears other dominant than *Clytia noliformis*. It might be assumed that this plant has a rate of growth and of disintegration higher than that of the other forms of holopelagic *Sargassum*, and that the *Clytia* is the only dominant able to keep pace with it. *S. natans II*, which occasionally is occupied by *Sertularia*, might be supposed to have a somewhat slower rate of growth and death; *S. fluitans X* and *S. natans IX*, which are often occupied by *Sertularia* or *Pasithea*, a still slower rate; *S. fluitans III* and *S. natans VIII*, which generally bear *Aglaophenia*, the slowest rate of all. Since *Clytia* appears to be able to utilize larger planktonts as food than can the Sertularian and Plumularian hydroids, the availability of these more motile organisms to *Clytia* might perhaps be assumed to be more reduced by the presence among the *Clytia* of close, repellant stands of Plumularians and Sertularians than would the availability of smaller organisms to the latter by the Campanularian. Such an effect might account for the infrequency with which *Clytia* dominates plants assumed to have a growth rate slow enough for the maintenance of *Sertularia* or *Aglaophenia*. The more efficient seive created by the growth-form of *Aglaophenia* might be considered to account for the more usual occurrence of this than of the Sertularians upon plants of growth rate sufficiently slow to permit the maintenance of *Aglaophenia*. Since the plankton of the Sargasso seas which can be utilized by hydroids is relatively sparse, it might further be assumed that a competition for food between intergrown colonies of different hydroids might occur, which would, other things being equal, favor the originally larger colony, in much the same way as a single shop has difficulty in meeting the competition of one which is a member of a chain. This initial difficulty in the replacement of an established by an invading form might reinforce infrequency of transfer in minimizing the occurrence of mixtures of dominant forms upon a single plant.

Direct evidence for the hypothetical relation between plant and epizoan tentatively outlined above is exceedingly difficult to obtain. Experiments at Bermuda suggested that *Clytia* may have a higher rate of linear extension than do the Sertularians and Plumularians, but were inconclusive. No clear indication of effective food competition in mixed stands of hydroids was obtained, but was perhaps hardly to be expected in the fertile neritic waters where the relatively few and short experiments were made. Nothing is directly known of the growth-rates of the different forms of pelagic *Sargassum*. The fact that the subfauna is more abundant on *S. fluitans III* than on *S. natans I* seems consistent with the assumption of a slower rate of growth and of disintegration in the former, since the subfauna seems clearly to depend for maintenance of its stock on the dissemination of new colonies rather than on continuous growth. It also seems consistent that the order of frequency and of thinness of habitus of the plants is more or less in direct ratio to their hypothetical rate of growth and disintegration. Various objections to the hypothesis, and numerous accessory points requiring explanation, which are not mentioned above, will it is expected be considered in detail in future essays on the remarkably complex animal community of pelagic *Sargassum*."

M. D. BURKENROAD, *in lit.*

In favor of Burkenroad's suggestion that dominance among the epizoans may be determined by the relationship between their rates of growth and the linear rate of growth of the plants, it may be pointed out that, even if we assume an equal volume or weight rate of growth for all forms of weed, e. g., in grams per week per kilogram, the absolute linear rates of growth (e. g., mm. increase in length per stem per week) would vary from one weed form to another approximately as assumed by Burkenroad as an explanation of epizoan dominance. Since it has the finest stems and leaves, *S. natans* (*I*) would have to add greater linear increases to its plant to give the same increase in weight per unit weight than would the somewhat coarser, *S. natans* (*II*). Still less linear increase would be required of the dense *S. natans* (*IX*) and least of all of the coarse *S. natans* (*VIII*) and of the *S. fluitans* series.

S. Natans SERIES

To give a general definition of the entire *S. natans* series seems a virtual impossibility. In difficult cases, especially when dealing with incomplete plants of certain forms of the *S. natans VIII* type, the complete absence of thorns on the stems becomes the sole determining feature by which the specimen can be assigned to the *S. natans* as distinct from the *S. fluitans* series. It might actually be said that every morphological feature shared in common by all members of the *S. natans* series are of purely negative character as indicated in the following diagnosis.

Receptacles absent. All branches of same general type. Cryptostomata absent or extremely scarce. Branches smooth, without thorns. Leaves simple, never forked, relatively straight, without conspicuous morphological twist, their costae distinct but without conspicuous ridge. Edges of leaves usually distinctly to strongly serrate.

It is evident that the preceding diagnosis is almost worthless apart from the elimination of forms which by the possession of characters *not* found in the *S. natans* series can be excluded from the latter, while it does not form a sound basis for positive identifications. With regard to all positive features such as leaf-size and form, and all characteristics of general habitus capable of expression in counts or measurements, the variations within the series are so great as to defy any attempt at giving a generalized definition for the whole series.

It might be stated that the leaves are generally very firm in comparison with leaves of similar width and thickness in benthonic forms, notably in comparison with *S. filipendula*, but also in comparison with most other benthonic species which have come to the writer's attention, except the more robust types of *S. pteropleuron*. But even this relative rigidity of foliage is not without exceptions, particularly among the more broad-leaved representatives of *S. natans* (*VIII*).

In view of this generally negative character of the common diagnosis of the entire group, it will be necessary for positive identification to make comparisons individually with every form comprised within its series. For this purpose the accompanying atlas has been arranged in descriptive sequence from the most narrow-leaved to the most broad-leaved specimens found in the available collections.

Abnormally produced leaves, not corresponding to the descriptions of typical plants given in the following, occasionally occur particularly in the basal portions of larger specimens, and are illustrated by an example of *S. natans* (*II*) given in figure 18 on page 38.

Silhouette 1 (figure 11) shows a typical, slender, fine-leaved specimen of *S. natans* (*I*), of moderate size (ab. 21 cm.), with distal spikes on every bladder, many of the spikes being narrowly foliate with a few serrations. Leaves 30–35 mm. long, about 1 mm. wide, sharply dentate. Bladders 2–2.5 mm. diameter, their pedicels 2–5 mm. long.

Silhouette 2 (figure 11) shows a small sprig of a broader-leaved variety of *S. natans* (*I*). Note the fully developed leaf arising from one of the bladders. Leaves 35–40 mm. long, 1.5–2.0 mm. wide, sharply dentate. Bladders 2–2.5 mm. diameter, their pedicels 2–4 mm. long.

Silhouette 3 (figure 11) shows a fragment of a still more broad-leaved specimen of *S. natans* (*I*), in which distal spikes are only present on a small minority of the bladders. Leaves 30–50 mm. long, 1.5–2.5 mm. wide, sharply dentate. Bladders about 3 mm. diameter, their pedicels short, only about 2 mm. or less.

Silhouette 4 (figure 11) finally shows a large (36 cm.) robust specimen of *S. natans* (*I*), in which many bladders completely lack distal spikes, and the spikes present on others are generally thin, simple and short. Leaves 35–45 mm. long, 1.5 (–2.0) mm. wide, sharply dentate. Bladders 3.0–4.0 mm. diameter, their pedicels 3–5 mm. long. It is evident that this specimen leads without any abrupt transition to:

Silhouette 5 (figure 11) which is a slender and narrow-leaved representative of *S. natans* (*II*), entirely free from bladderspikes and quite typical of numerous other representatives of the finer varieties of this form. Leaves 50–60 mm. long, sharply dentate, 1–1.5 mm. wide. Bladders about 3 mm. diameter, their pedicels about 2 mm. or less.

Silhouette 6 (figure 12) shows a slightly more luxuriant representative of *S. natans* (*II*) than that shown in silhouette 5. Leaves 50–70 mm. long, 1.5–2.0 mm. wide, sharply dentate. Bladders 3–4 mm. diameter, their pedicels 1–3 mm. long.

Since *S. natans* forms a continuous series of intergradations so far as leaf and plant form is concerned, one might, on the basis of the plants alone, be inclined to extend the range of modifications covered by the designation *S. natans* (*II*) to include also several of the relatively narrow-leaved forms shown in the following silhouettes. But, on the basis of the epizoans as identified by Burkenroad, the typical dominants of *S. natans* (*VIII*) (*Aglaophenia*) are present already on the specimens shown in silhouettes 8, 9, and the following figures. Taking epizoans into consideration, we therefore restrict *S. natans* (*II*) to the narrow range shown by silhouettes 5 and 6 (epizoan: *Clytia*), and this is the form, only slightly coarser than *S. natans* (*I*), in which the weeds without bladderspikes most commonly occur in the open Atlantic.

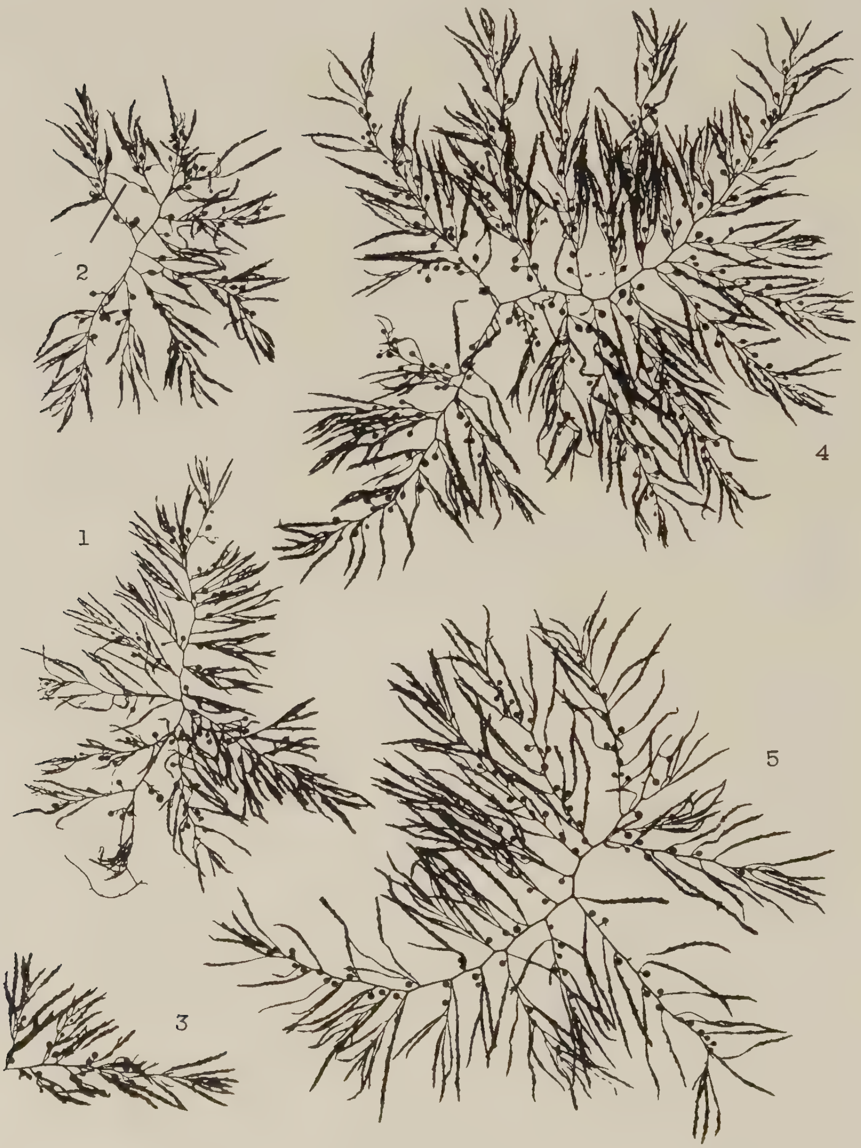


Figure 11. Silhouettes 1–4: *Sargassum natans* (*I*). Silhouette 5: *S. natans* (*II*), slender variety. Scale see figure 12.

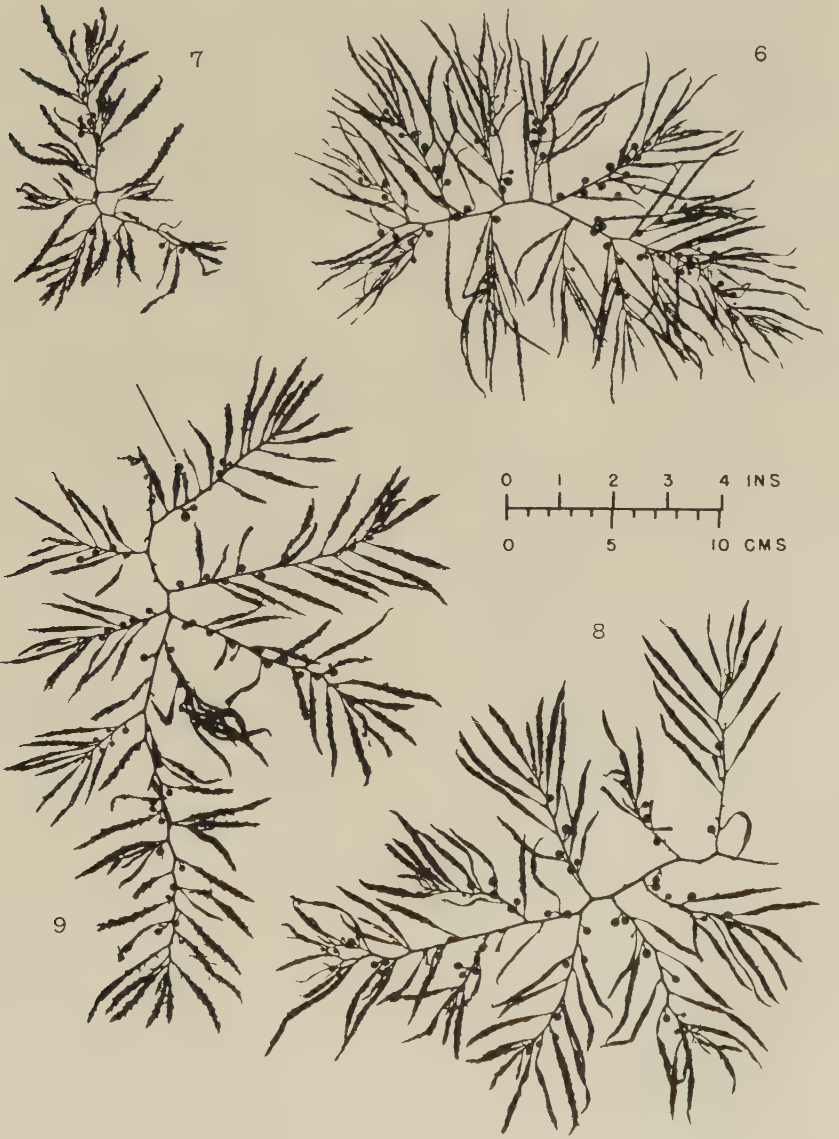

7
6
0 1 2 3 4 INS
0 5 10 CMS
8
9

Figure 12. Silhouettes 6–7: *Sargassum natans* (II). Silhouettes 8–9: *S. natans* (VIII) See text.

Silhouette 7 (figure 12) shows a similar variation towards broader and softer foliage in *S. natans* (*II*) as that shown by silhouette 3 in *S. natans* (*I*). Leaves 40–50 mm. long, 2.5–3 mm. wide, sharply dentate. Bladders about 3.0 mm. diameter, their pedicels 2 mm. long or less. This specimen has also been found by Burkenroad to have an atypical epizoan fauna dominated by *Sertularia*.

A somewhat divergent, more densely foliate variety of *S. natans* (*II*), with extremely sharply dentate, but quite narrow leaves and relatively numerously retained bladders is shown in silhouette 22 (figure 16, p. 34) for comparison with *S. natans* (*IX*).

Silhouettes 8 and 9 (figure 12) represent very narrow-leaved specimens of *S. natans VIII*, so designated on the basis of their epizoan fauna (dominant: *Aglaophenia*). Leaves 50–60 mm. long, 3–3.5 mm. wide, sharply dentate (9) or rather weakly serrate (8). Bladders about 4 mm. diameter, pedicels about 2 mm. Silhouette 9 shows a bladder in a terminal position on a leaf or foliate pedicel 17 mm. long.

Since epizoan fauna could not regularly be taken into consideration in mass sorting on shipboard, it is evident from subsequent determinations on preserved material that many of these narrow-leaved *S. natans VIII* have been entered in the field records as *S. natans II*. This discrepancy between field records and final determinations mainly affects the data from the waters near the coast of the West Indian Islands and within the Central American Seas but is not significant for the open Atlantic, in which the bulk of the weeds without bladderspikes of the *S. natans* series occurs in the typical form of *S. natans II* shown in silhouettes 5 and 6.

In silhouette 10 (figure 13) an increase in leaf width and coarseness is noted. Leaves 40–55 (65) mm. long, 3.5–4.0 mm. wide, moderately dentate. Bladders 3–4 mm. diameter, their pedicels 1–2.5 mm. long, except when alate or foliate, when they may be as much as 20 mm. long. Silhouette 10 shows several narrowly alate pedicels, and one broadly foliate with dentate margin and with the terminal vesicle carrying a long, slightly foliate distal spike.

Silhouettes 11–13 show further variations of *S. natans VIII* with moderate leaves. In silhouette specimen 11 the leaves are fairly short and blunt, 40–50 mm. long, 3.5–5.0 mm. wide, and sharply dentate. Bladders small, 2.5–3.0 mm. diameter, on 1–3 mm. pedicels. In specimen 12 the leaves are longer and more pointed, 50–60 mm. long, 3.5–4.0 mm. wide. Bladders 3.5–4.0 mm. diameter, on 2–4 mm. pedicels.

Silhouette 14 (figure 14) represents a very vigorous specimen of *S. natans* (*VIII*), in which the comparatively narrow and pointed leaves still point towards the intergradation with *S. natans* (*II*). Leaves 40–50 mm. long, 3.5–4.5 mm. wide. Bladders 4 mm. diameter on 1–3 mm. pedicels.

Silhouettes 15–17 (figure 14) show an assortment of moderately robust but quite typical *S. natans* (*VIII*) with relatively short and broad leaves, which

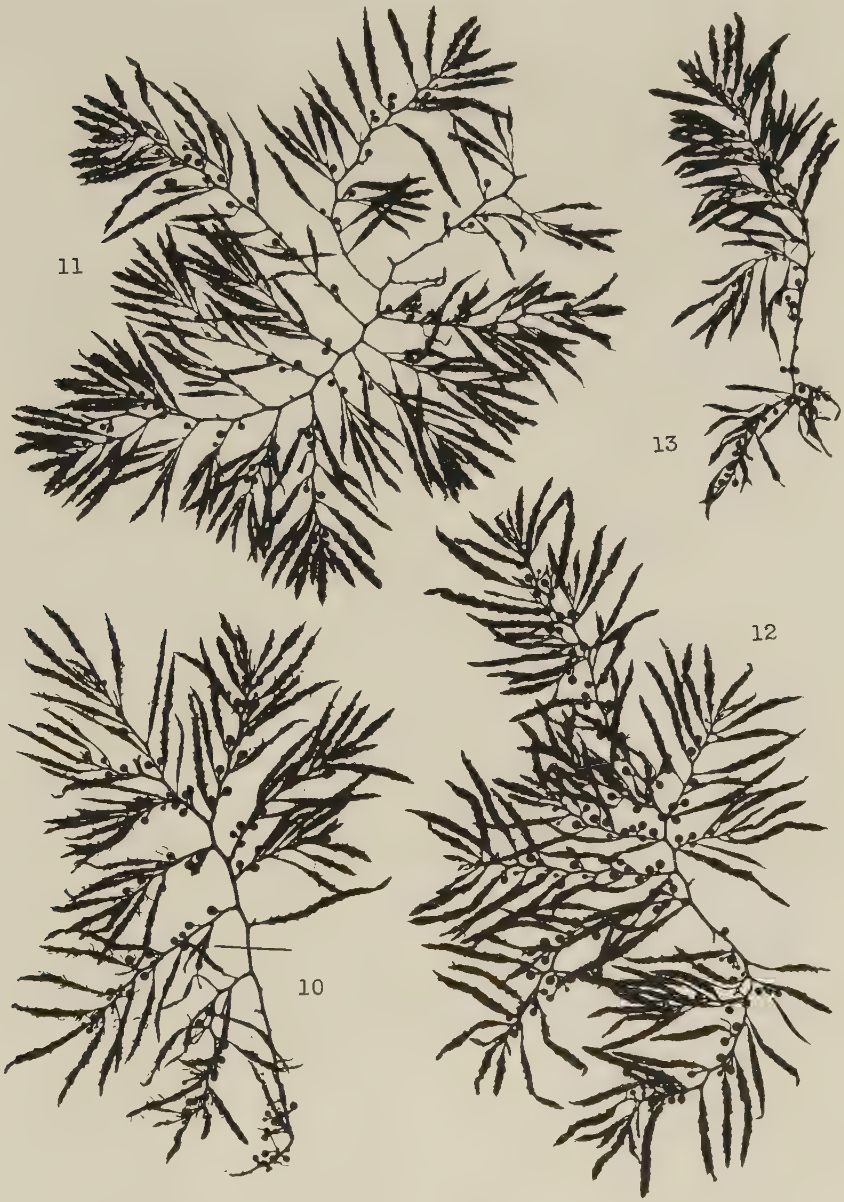


Figure 13. Silhouettes 10–13: *Sargassum natans* (VIII). See text. Scale, see figure 16.

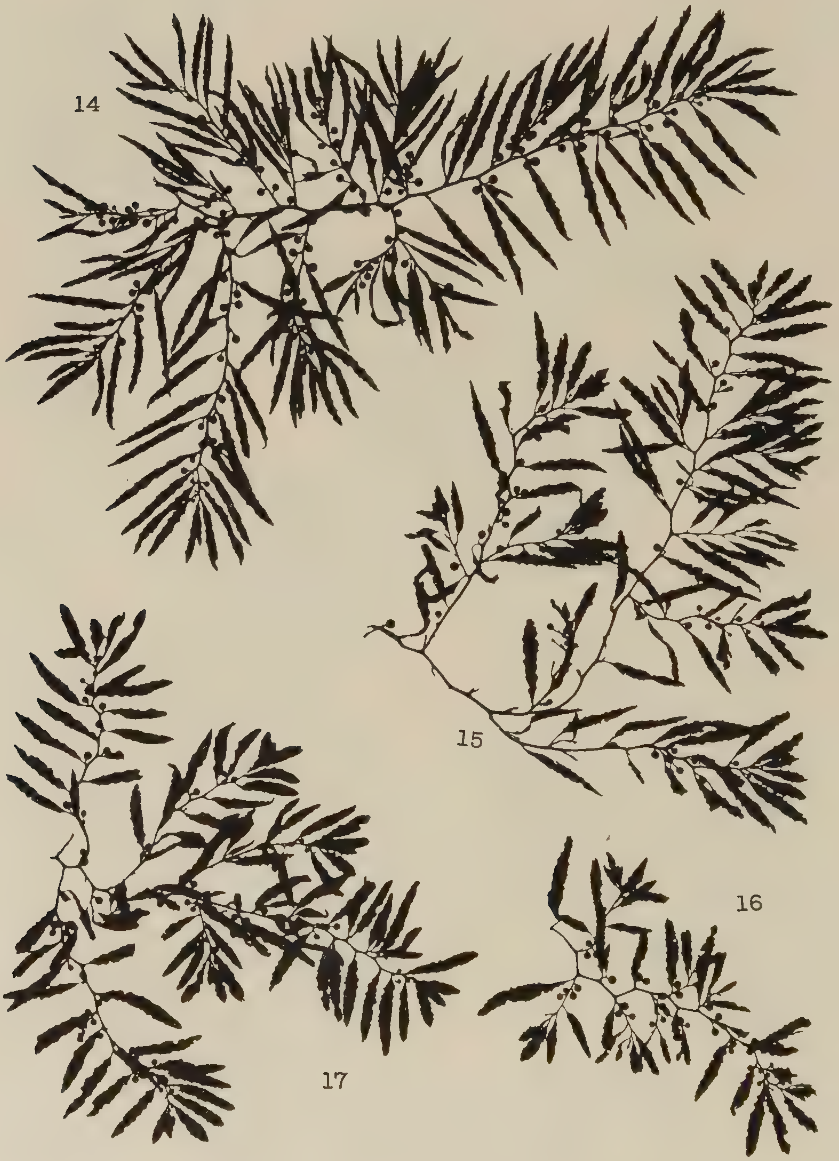


Figure 14. Silhouettes 14–17: *Sargassum natans* (*VIII*)). Scale see figure 16.

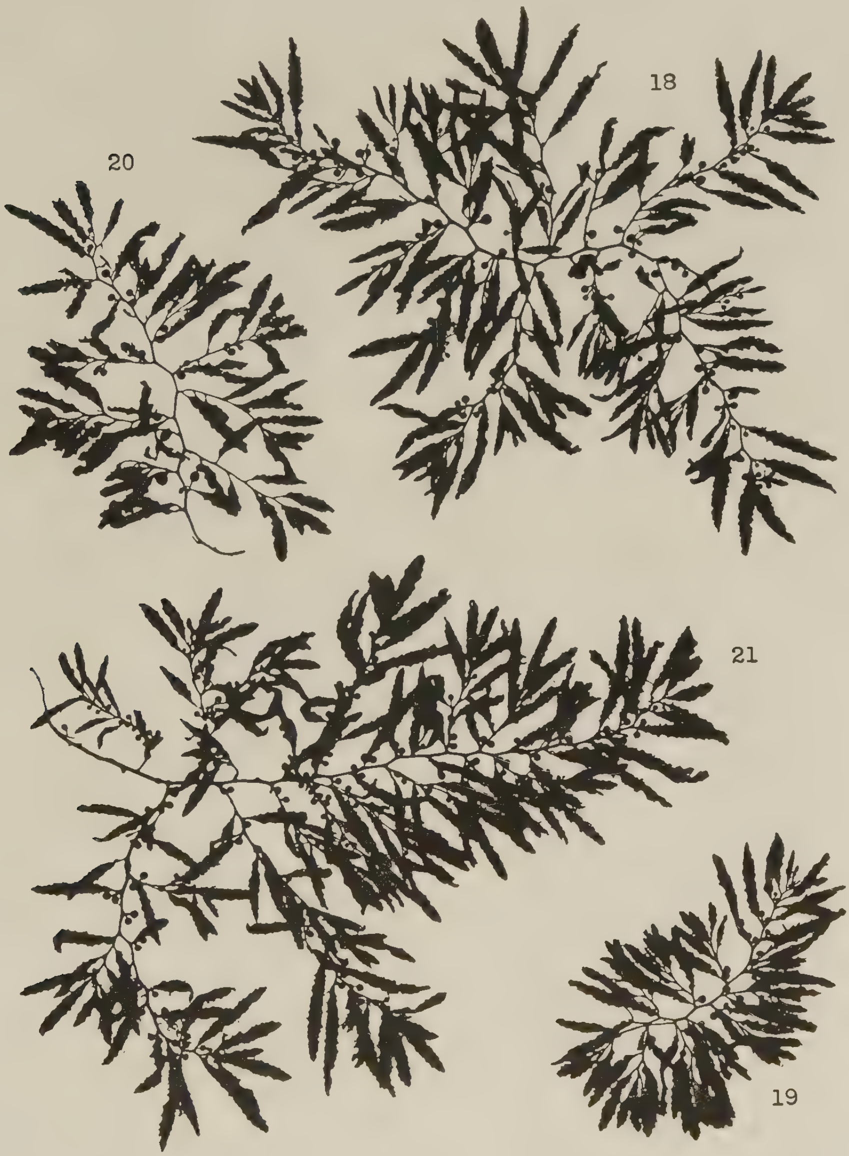


Figure 15. Silhouettes 18–21: Typical, broad-leaved *Sargassum natans* (*VIII*). Scale see figure 16.

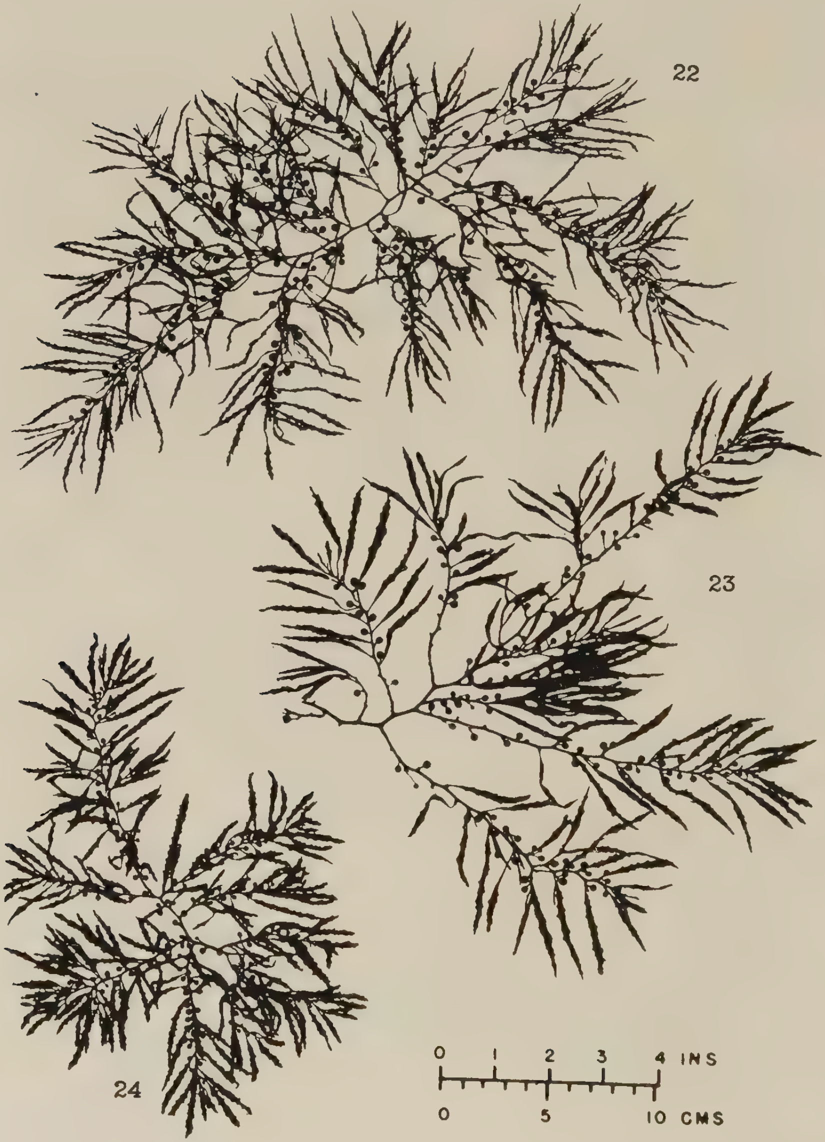

22
23
24
0 1 2 3 4 INS
0 5 10 CMS

Figure 16. Silhouette 22: *Sargassum natans* (II) and silhouette 23: *S. natans* (VIII), for comparison with silhouette 24: *S. natans* (IX).

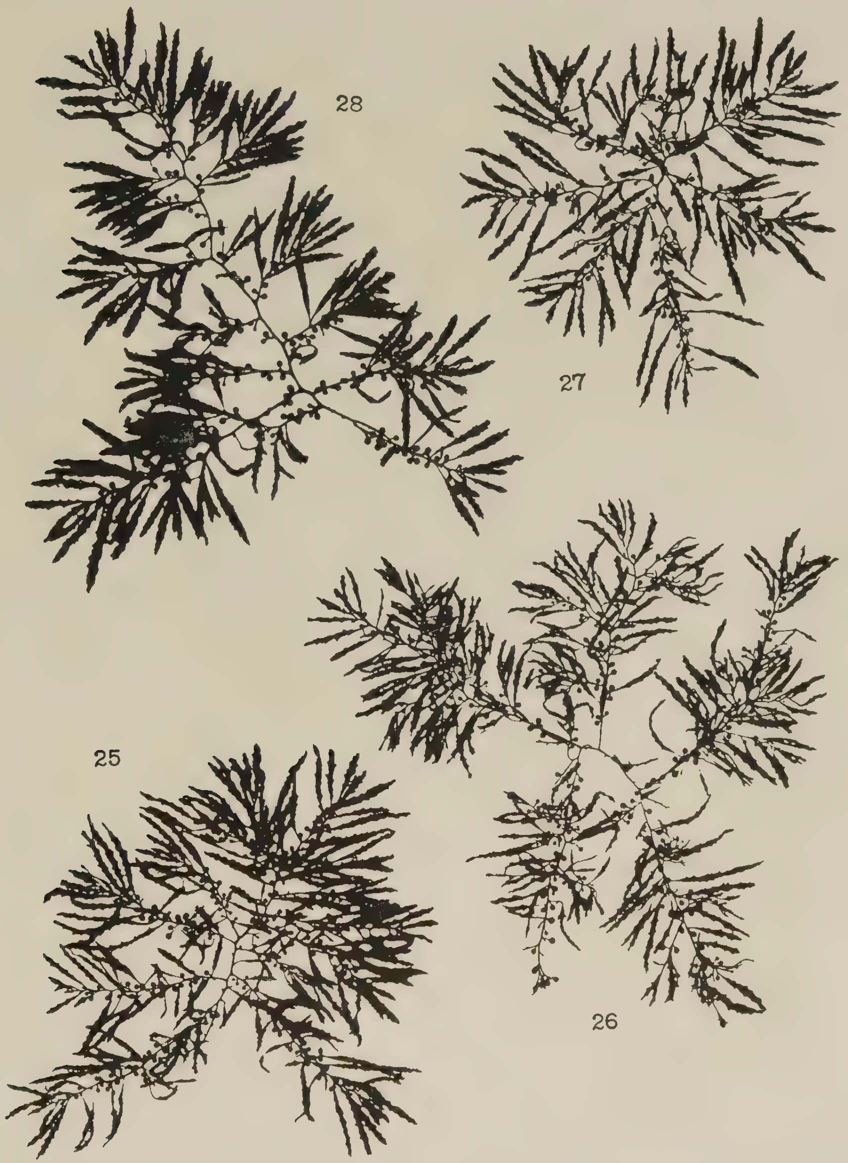


Figure 17. Silhouettes 25–27: *Sargassum natans (IX)*. Silhouette 28: Transition from *S. natans (IX)* to *S. natans (VIII)*. Scale see figure 16.

integrate with *S. natans* (*II*) through such intermediates as that shown in silhouette 11 (figure 13). Leaves 40–45 mm. long, 5–6 mm. wide (Nos. 15 and 17), 6–7 mm. wide (No. 16). Bladders 3–4 mm. diameter, on 1–2 mm. pedicels.

Silhouettes 18–21 (figure 15) finally illustrate various examples of luxuriant *S. natans* (*VIII*) at the end of this series. Leaves 35–45 mm. long (Nos. 18–20), 45–55 mm. long (No. 21), 5–6 mm. wide (Nos. 18–20), 6–7 mm. wide (No. 21). Bladders 3–4 mm. diameter, on 1–2 mm. pedicel. No. 18 with one slightly alate pedicel 4 mm. long with one denticulation.

Silhouette 22 (figure 16) shows a comparatively densely foliate variety of *S. natans* (*II*), with moderate, narrow, sharply dentate leaves and comparatively numerously retained bladders, pointing towards *S. natans* (*IX*). Leaves 45 mm. long, 1–1.5 mm. wide. Bladders 2.5–3 mm. diameter, on pedicels 1–3 mm. long.

Silhouette 23 (figure 16) shows a robust specimen of *S. natans* (*VIII*) of the same general type as that shown in silhouette 9 (figure 12), but with more numerous bladders. Apart from the latter feature, silhouette 23 is here given for its contrast with rather than its resemblance to *S. natans* (*IX*). Leaves 50–55 mm. long, 2.5–4 mm. wide. Bladders 3–3.5 mm. diameter, on pedicels 1–3 (7) mm. long.

Silhouettes 24–27 (figures 16–17) give typical examples of *S. natans* (*IX*), with its small, sharply dentate leaves, dense growth, numerous bladders, etc., which clearly show the actual distinctness of this form from all other members of the *S. natans* series illustrated in this report. Leaves 30–40 mm. long, 2–3 mm. wide. Bladders 1.5–2.5 mm. diameter, on pedicels 1–2 mm. long.

In silhouette 28 (figure 17), we have a specimen caught in the same haul as the others shown in figure 17 which combines the profuse foliation and numerous small bladders of *S. natans* (*IX*), with a leaf-size and form pointing clearly towards such representatives of *S. natans* (*VIII*) as that shown in silhouette 11 (figure 13, page 31) while its relations are still further complicated by the presence of long, foliate, distal spikes on several of its bladders. Leaves 40–45 mm. long, 2–4 mm. wide. Bladders small, 2–2.5 mm. diameter, on 1–2 (4) mm. pedicels.

S. Fluitans SERIES

The group here referred to under the taxonomic designation of *S. fluitans* Börgesen seems much simpler than the *S. natans* series in the sense that its variations, apart from the dimorphism to be described below, seem to be individual rather than serial and systematic. The entire range of individual variations with reference to leaf form, etc. in *S. fluitans* is also narrower than the range of serial variations in *S. natans*. It is therefore possible to give the general definition of the *S. fluitans* series a more positive form than that given in the diagnosis of *S. natans*, as follows:

Receptacles absent. Branches with thorns, frequently extending to the pedicels of the bladders, but sometimes quite scarce and mainly observable only near the actively growing distal ends of the branches. Leaves[1] typically 4–5 mm. apart, usually simple, very rarely forked, their width usually 3–5 mm., normally contained about 5–12 times in their length, which usually varies between 20 and 60 mm.[2] Cryptostomata almost always present at least on some of the leaves, sometimes on all, but always small, inconspicuous and irregularly arranged. Costae distinct, but without conspicuous ridge. Edges of leaves vaguely dentate to strongly serrate.

The separate plants of *S. fluitans* occur chiefly in two typically quite distinct forms, of which we shall here begin with the description of the form designated as *S. fluitans* (*X*).

In its typical form *S. fluitans* (*X*) is most conspicuously characterized by its general habitus which is that of a dense, globular or oblong cluster, of quasi-radially arranged, short, subequal, richly foliate, branches. The overall length of such plants is usually only about 20 cm. or less and rarely exceeds 30 cm. in any direction. The branches on the *average* originate less than 6 mm. apart. The leaves are relatively short, usually less than 50 mm. long,[3] and typically only about 30 mm. or less, although average leaf lengths approaching 50 mm. is occasionally characteristic of specimens with a general habitus entirely typical of *S. fluitans* (*X*). The leaves are thick, comparatively very firm, and relatively straight and flat, without conspicuous morphological twist. In fresh material they also differ from the leaves of *S. fluitans* (*III*), in being of a dark olivaceous green color, instead of yellowish brown. Cryptostomata seem to be always present, and indeed fairly numerous, although inconspicuous and irregularly arranged. The edges of the leaves are typically less sharply serrate than in *S. fluitans* (*III*), although the serrations are extremely variable and always distinct. While most of the bladders are smooth at the distal end, typical specimens often show a number of aristate vesicles with the apical point sometimes continued into a fully formed leaf up to 20 mm. length. The pedicels of the bladders also frequently show an unusual length (up to 9 mm., at least), although their length is normally only about 2–5 mm. In this *variability* of the vesicles, their pedicels and apical appendages rather than in their usual form *S. fluitans* (*X*) seems to differ from *S. fluitans* (*III*), as it also does by its typically much more abundant cryptostomes and by the other features mentioned in the preceding. An epizoan species occurring exclusively on *S. fluitans* (*X*) is mentioned by Burkenroad on page 23.

---

[1] Only leaves sufficiently far below the distal end of the branch to be considered fully developed are taken into account in this description.

[2] As also in the *S. natans* series, exceptionally long leaves exceeding 80 mm. length are occasionally found in the basal portions of the plant (see figure 18). These exceptional leaves would appear to have had an increased growth in length only and therefore show a very high ratio between width and length (1 : 20 or more). But since there are rarely more than a single or a couple of these long leaves present on any single specimen, they do not contribute significantly to its general appearance.

[3] Leaves of exceptional length occur also in this form.

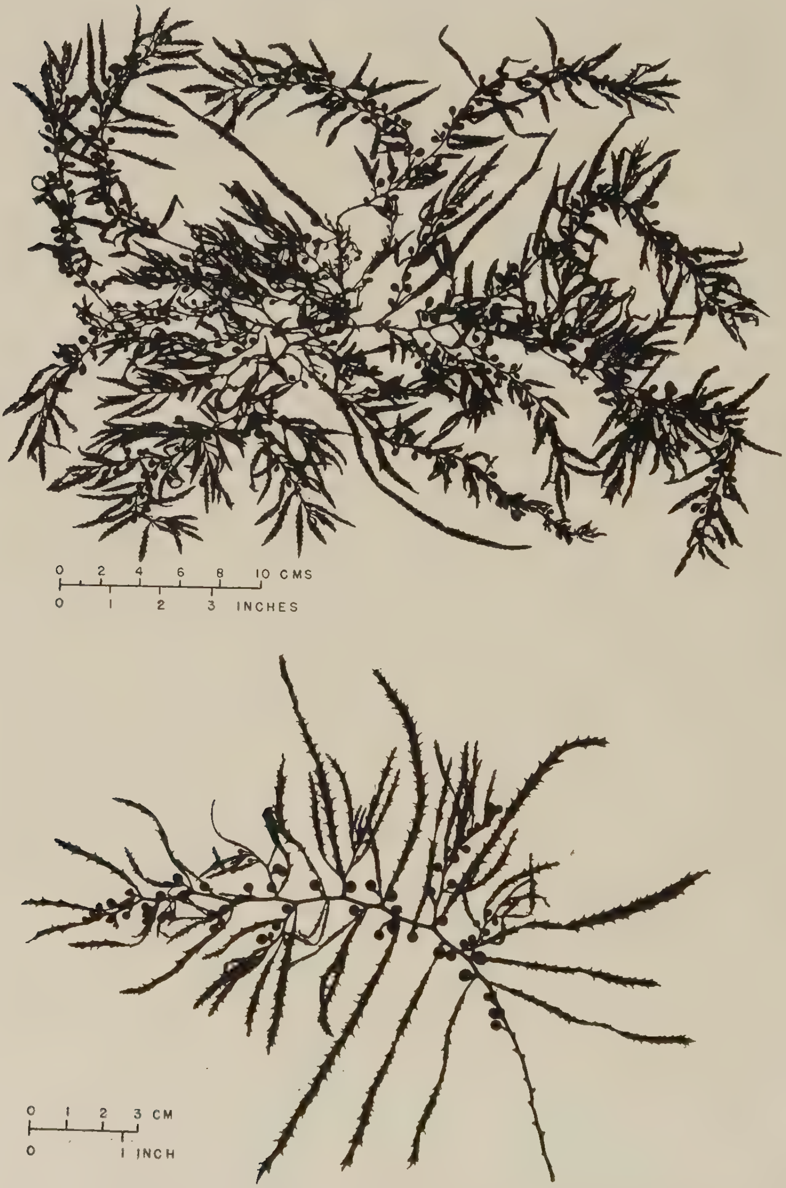

0 2 4 6 8 10 CMS
0 1 2 3 INCHES
0 1 2 3 CM
0 1 INCH

Figure 18. Herbarium silhouettes showing abnormally produced leaves in *Sargassum fluitans* (*III*), above; and in *S. natans* (*II*), below.

From its more typical form described in the preceding and illustrated in fig. 4, *S. fluitans* (*X*) shows numerous individual variations illustrated in figs. 19–20.

Figure 19 shows various specimens of typical *S. fluitans* (*X*) of more or less circular or slightly oblong[1] shape without differentiation of major (main) and minor stems or primary branches. Considerable variation of leaf form and size may be noted even within this relatively homogeneous group. Silhouette 29, overall length 37 cm.; leaves 25–40 mm. long, 3–4.5 mm. wide. Bladders 4–6 mm. diameter, circular or ovate, a few with small distal spikes, one with distal spike broadly foliate. Silhouette 30, 15 cm. overall, leaves and bladders as in No. 29. Silhouette 31, length 20 cm., represents a variety with slightly more slender growth. Leaves usually not over 4 mm. wide, 30–40 mm. long, with more distinct midrib than in the forms with blunter leaves. Silhouette 32, 30 cm. overall, has generally smaller leaves than the other specimens shown in figure 19, the length of the leaves being predominantly less than 25 mm., although a few reach 35 mm., their width predominantly 2–2.5 mm., exceptionally 4 mm. Silhouette 33, on the other hand, shows a long-leaved variety of *S. fluitans* (*X*), with leaves 45–60 mm. long but only 2–2.5 mm. wide.

Figure 20 shows various examples of *S. fluitans* (*X*) of looser growth, pointing towards *S. fluitans* (*III*). These specimens all have naturally fairly flat, straight and thick leaves and would all, on the basis of fresh material, without hesitation be sorted with *S. fluitans* (*X*). Silhouette 34 shows the large, strongly ovate bladders (up to 6 mm. largest axis) which seem particularly common on the more luxuriant plants of *S. fluitans* (*X*). The leaves are 35–50 mm. long, 3.0–4.5 mm. wide, with not very strongly serrate margins. A bifurcated leaf is conspicuously shown. Silhouette 35 agrees with 36 in foliage, etc., differing only in its general habitus. Silhouette 36 shows a rather aberrant form with straight, narrow, only weakly serrate leaves, 35–40 mm. long and 2–2.5 mm. wide. The type of growth is also unusual, and the cryptostomata slightly less inconspicuous and more regularly arranged than normal for *S. fluitans* (*X*). It is not without hesitation that this plant is included in the *S. fluitans* (*X*)? series, not as part of its intergradations but rather as a divergent extreme variety.

Silhouette 37 shows a nearly isodiametric, fairly typical, though rather loosely grown, plant of *S. fluitans* (*X*) in which one single branch has been produced to assume the appearance of *S. fluitans* (*III*). With regard to general habitus, the "basal" part of No. 37 compares with such specimens as No. 35. With regard to leaf size, form and texture it is in perfect agreement with No. 31. Leaves 25–35 mm. long, 25–35 (40) mm. wide. While the produced branch if

---

[1] The oblong shape of the two larger specimens is due to a selection of plants of this form to fit the herbarium sheet rather than to a normal preponderance of elongate over iso-diametric form with larger size.

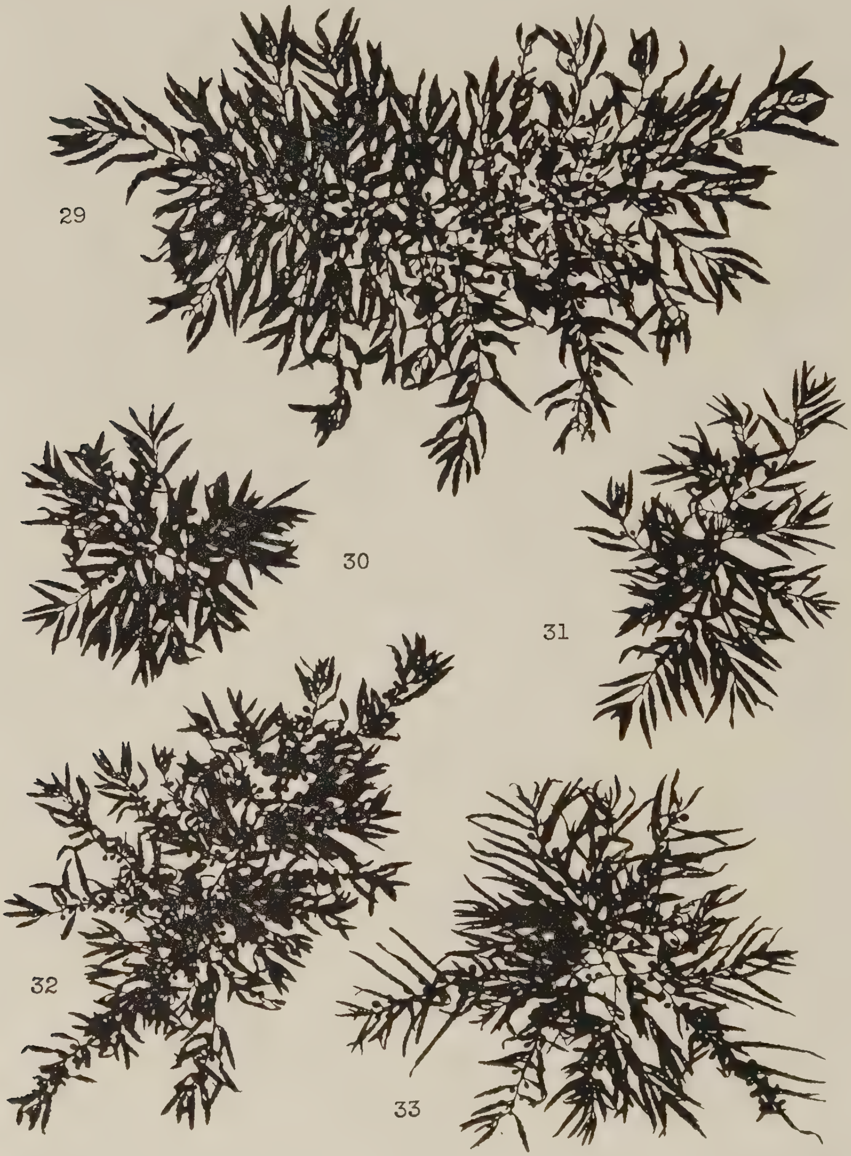


Figure 19. Silhouettes 29–33: *Sargassum fluitans* (*X*). Typical dense growth. Scale see figure 21.

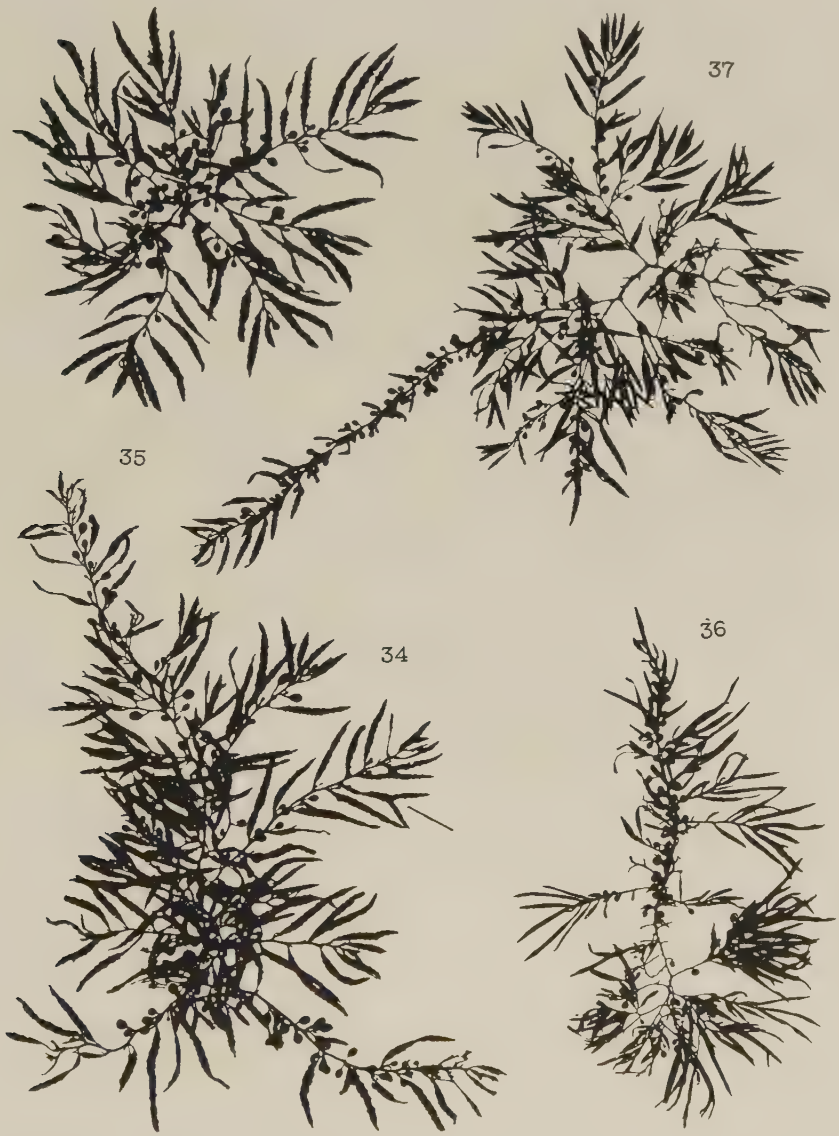


Figure 20. Silhouettes 34–36: *Sargassum fluitans* (*X*). Looser growth. Silhouette 37: *S. fluitans* (*X*) and *S. fluitans* (*III*) on same plant. See text. Scale see figure 21.

separated from the basal branches would unhesitatingly have been classified as a fragment of some such typical representative of *S. fluitans* (*III*) as that shown in silhouette 43.

Several larger examples (too large for herbarium preservation) in which still more fully developed and branched stems of *S. fluitans* (*III*) are organically connected with still more typical, dense clusters of *S. fluitans* (*X*) are available in liquid preservation.

S. fluitans (*III*) is typically very easily distinguished from *S. fluitans* (*X*) by its loose, open and stringy general habitus, dominated by one or several long main branches sharply differentiated from the much shorter and subordinate secondary branches which generally originate *on the average* more than 6 mm., typically around 7 mm., apart. The plants may reach an overall length between ends of main branches approaching 1 meter and usually occur in sizes of 30 cm. or more in any region of vigorous growth. The leaves are usually longer than in *S. fluitans* (*X*), generally more than 30 mm., typically 40–60 mm. long in well-developed specimens, with the width (typically 4–5 mm.) usually contained 8–12 times in their length. The leaves are crisp and firm but not so thick as in *S. fluitans* (*X*), typically conspicuously twisted and curled, the twisting and curling being more pronounced the more luxuriant the general appearance of the plant. Color in fresh plants yellowish brown (light tobacco brown). Cryptostomata often absent from single leaves but very rarely absent from all leaves on a plant of reasonable size. They also commonly occur throughout the foliage but are usually much fewer on each leaf than in typical representatives of *S. fluitans* (*X*). Edges of leaves usually sharply serrate. Bladders without spikes, smoothly rounded at apical end, on short pedicels, normally less than 3 mm. long.

The specimens classified as *S. fluitans* (*III*) also show a considerable diversity of individual variations particularly with regard to general appearance of foliage and abundance of thorns on the stems.

Figure 21 shows various luxuriant examples of typical *S. fluitans* (*III*). Leaves 45–60 mm. long (35–45 mm. in No. 40), and 4–5 mm. wide.

Figure 22 illustrates the intergradations toward smaller and narrower leaves, and variations in general habitus. In No. 42 leaves are 35–45 mm. long, and about 4 mm. wide. In No. 43, 35–40 mm. long, and 3–3.5 mm. wide. On No. 44 about 35 mm. long, and 2.5–3 mm. wide.

Figure 23 shows several examples of the finer-leaved forms of *S. fluitans* (*III*) (Nos. 45–48) and compares these with specimens of the *S. natans* series of the same general appearance. No. 45 is a densely foliate branch of *S. fluitans* (*III*), with leaves 30–40 mm. long, 2.5–3.5 mm. wide. No. 46 is a quite common, slender and rather sparsely foliate type with leaves about 35 mm. long, 2–3 mm. wide. The actual specimen represented in silhouette 47 is in some respects intermediate between *S. fluitans* (*III*) and *S. fluitans* (*X*) with regard to foliage

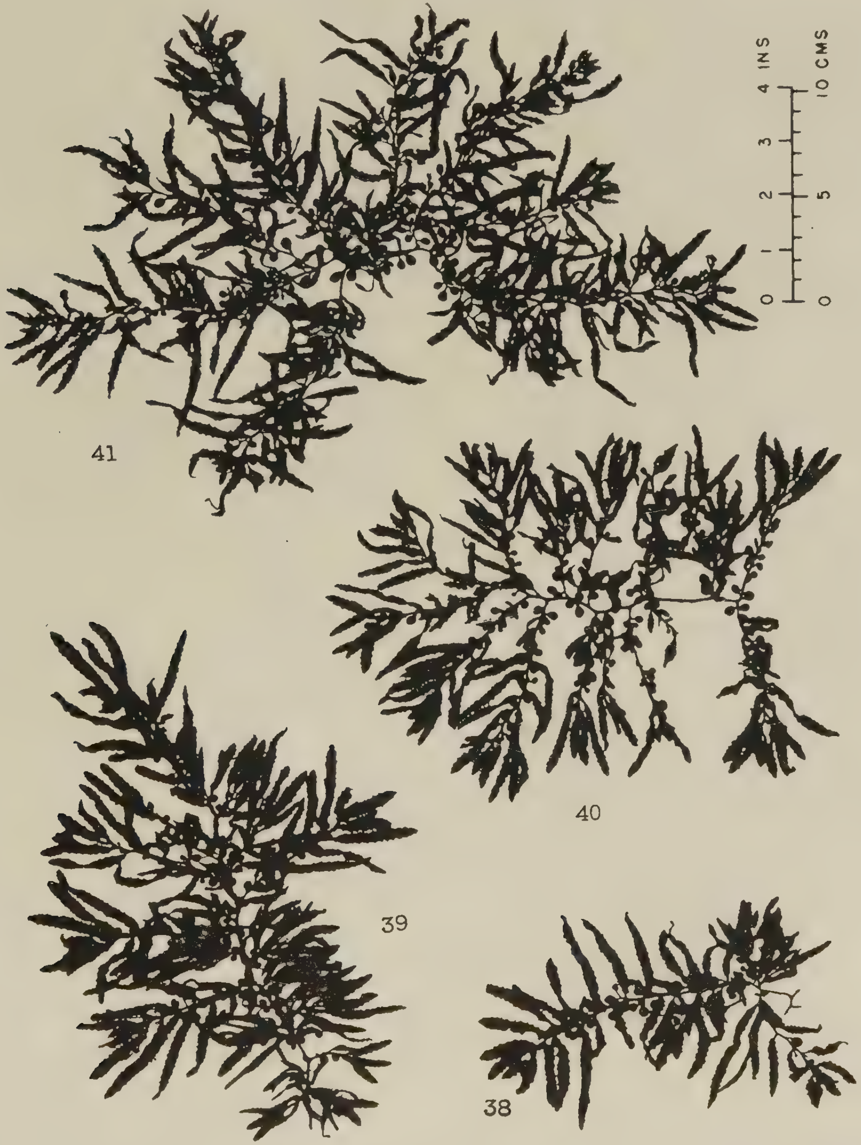

0
1
2
3
4 INS
0
5
10 CMS
41
40
39
38

Figure 21. Silhouettes 38–41: ***Sargassum fluitans (III).*** **Luxuriant, broad-leaved specimens.**

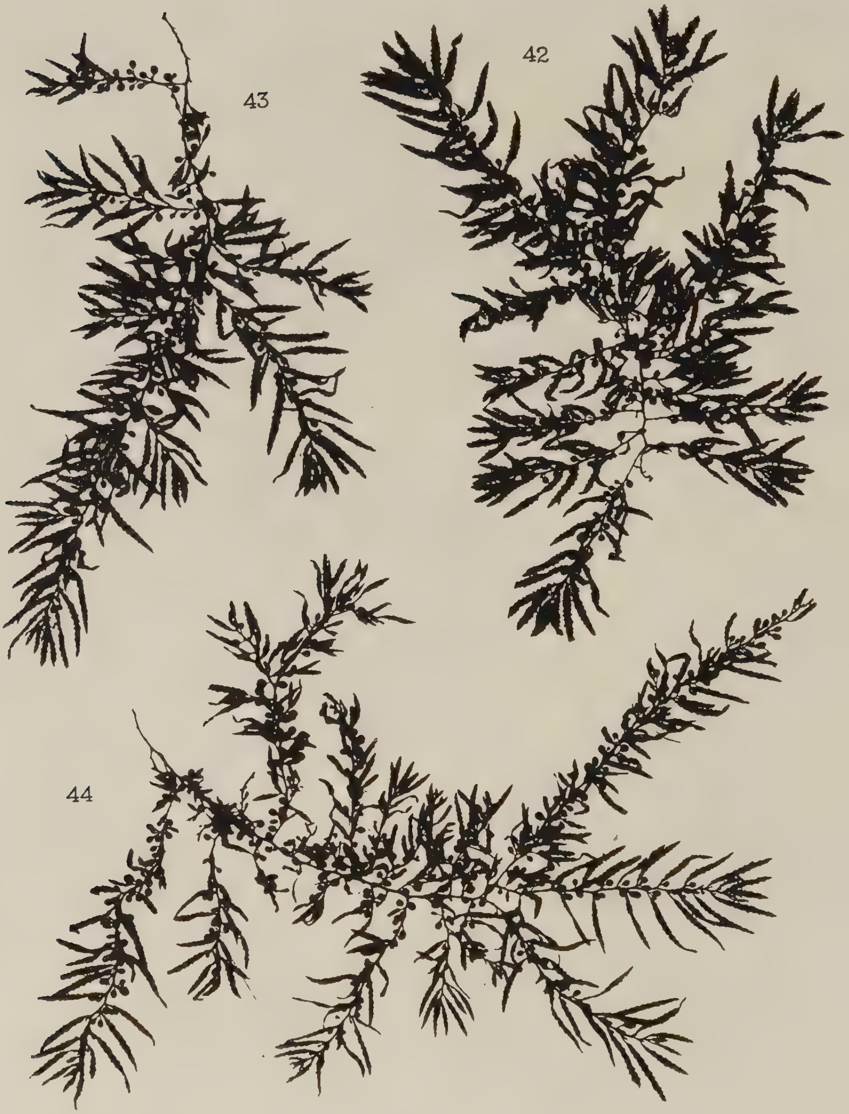


Figure 22. Silhouettes 42–44: *Sargassum fluitans (III)*. Slender, narrow-leaved specimens. Scale see figure 21.

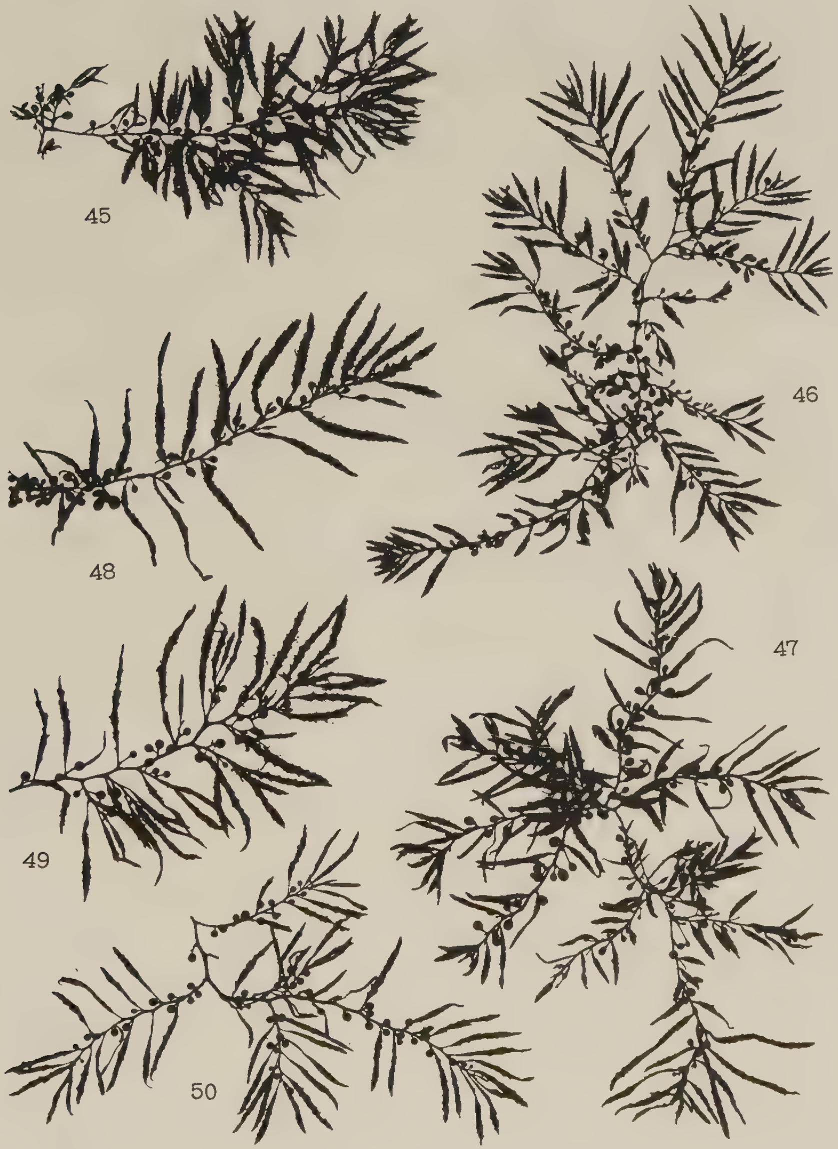


Figure 23. Silhouettes 45–47: Slender specimens of *Sargassum fluitans* (*III*) for comparison with similar specimens of *S. natans* (*II–VIII*) shown in silhouettes 49–50. Scale see figure 21.

and general type of growth. Leaves 35–50 mm. long, 2–2.5 mm. wide. No. 48 is a single stem of a very long-leaved *S. fluitans* (*III*), presented for comparison with a long-leaved branch from the *S. natans* series shown in silhouette 49. Leaves (of No. 48) 50–60 mm. long, 3.5–4.5 mm. wide.

Silhouettes 49–50 belong to the *S. natans* series (narrow-leaved (*VIII*), or broad-leaved (*II*)). In No. 49 leaves are 50–65 mm. long, 3–4 mm. wide. In No. 50 leaves are about 35 mm. long and 2.5–3 mm. wide. Comparisons of No. 50 with Nos. 46 and 47, and between Nos. 48 and 49 will probably sufficiently illustrate how even the differentiation between *S. fluitans* and *S. natans* may come to seem quite arbitrary for specimens of *S. fluitans* in which only a few minute thorns may be discovered on their stems by close examination. It seems characteristic, particularly of the slender varieties of *S. fluitans* similar to that shown in silhouette 46 (although not true of this particular specimen), that the thorns on stems and branches may not uncommonly be greatly reduced both as to numbers and sizes. This tendency towards a relative smoothness of stems seems associated with a reduced apparent vigorousness of the entire plant, so that a close inspection of each specimen to differentiate between *S. fluitans* and similar members of the *S. natans* series is much more often required in the marginal zones of the pelagic vegetation (as, for instance, in the Gulf of Mexico during the cold season) than in the Sargasso Sea proper, and in the Cayman and Caribbean seas.

PRELIMINARY DISCUSSION OF RELATIONSHIPS

In the preceding we have described how the *S. natans* group forms a single continuous series of intergradations in the manner indicated in our figure. While the derivation of such a series might have occurred from either direction, *S. natans* (*VIII*) is, in the author's opinion, the form most suggestive of benthonic origin both from the point of view of its geographical distribution (p. 66) and its morphological character, which frequently recalls the irregular growth of sessile plants to a much higher degree than does any of the other extremely regular pelagic forms of the *S. natans* series. In this statement the author has in mind the commonly observed lack of equivalence in *S. natans* (*VIII*) between branches of the same order originating near each other from a common stem. Occasionally this lack of equivalence extends beyond a mere difference in size and general appearance between such branches, to a perceptible difference in the form of their leaves. This lack of equivalence between branches of the same order also quite frequently expresses itself very conspicuously in the general appearance of the entire plant by a complete disruption of the pattern of fairly regular and quite gradual decrease in the size of the branches originating along the main stem from its basal to its distal end. In all other forms of *S. natans* adjacent branches from the main stem will usually be found to be of approximately the same general size and appearance and their size will show a gradual decrease towards the tip of the main stem. While this is, of course, also frequently true of *S. natans* (*VIII*), it seems definitely impossible to claim that this is any general rule for that form in anything like the extent to which it is true of the others. Under otherwise equal circumstances such irregularities should suggest orientation in three dimensions rather than to a linear axis in one dimension only.

Without pretending to claim that it amounts to much more than a personal guess, the writer would therefore be inclined to look for the derivation of the entire *S. natans* series through *S. natans* (*VIII*).

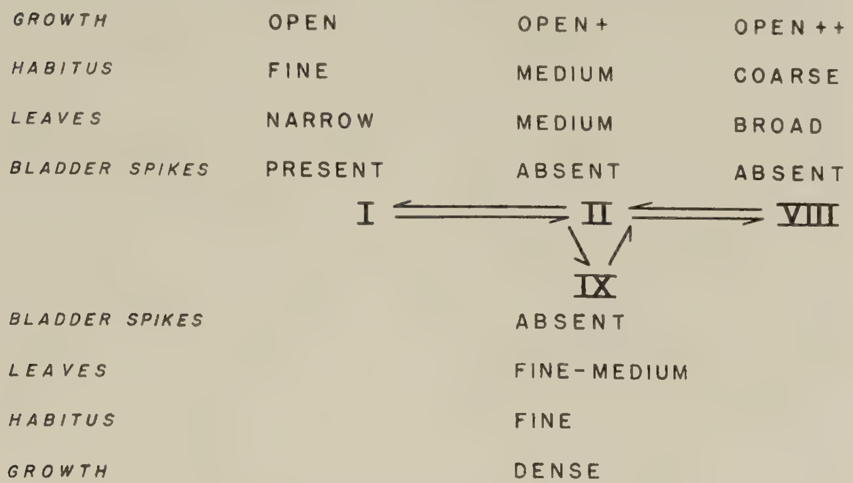

GROWTH
OPEN
OPEN +
OPEN ++
HABITUS
FINE
MEDIUM
COARSE
LEAVES
NARROW
MEDIUM
BROAD
BLADDER SPIKES
PRESENT
ABSENT
ABSENT
I
II
VIII
IX
BLADDER SPIKES
ABSENT
LEAVES
FINE-MEDIUM
HABITUS
FINE
GROWTH
DENSE

Figure 24. Table illustrating apparent intergradations in *Sargassum natans*. Features given are those of typical representatives of each form.

In the preceding description we have already mentioned that there are cases in which the differentiation between a relatively robust but narrow-leaved *S. natans* (*VIII*) and a slender and nearly smooth-stemmed *S. fluitans* (*III*) also seems to become quite arbitrary. It is probably unlikely that the true *S. natans* (*VIII*) could actually have been derived from *S. fluitans*, and the author merely wishes to state that he has not been able to satisfy himself that this possibility can be entirely excluded on a morphological basis, and that confusions may occasionally arise in the identification, particularly of smaller specimens or fragments, on the borderline between *S. natans* (*VIII*) and *S. fluitans* in general appearance.

In the *S. fluitans* group we also find a considerable variation in general appearance which has been sufficiently described in the preceding and only two features remain for discussion here, namely, the interesting dimorphism shown by this species in its floating state and the single fertile specimen which apparently can be referred to this form without serious hesitation.

The dimorphism between *S. fluitans* (*III*) and (*X*) may seem insignificant when described in words and pictures only, but in the fresh material the difference is typically so striking that the two forms were without difficulty segregated for weighing in the routine sorting of the hauls from the beginning of the investigation long before the proper status of *S. fluitans* (*X*) had been established by a more critical examination of long series of samples. Among the healthy weeds in the Sargasso Sea proper, *S. fluitans* (*X*) could, as a matter of fact, undoubtedly have been sorted from the rest blindfolded, by a mere feeling of its form and the characteristic stiffness or crispness of touch by which it differs from the thinner leaves and more flexible form of *S. fluitans* (*III*). The general differences between *S. fluitans* (*III*) and (*X*) have been sufficiently described on p. 37. Occasionally we find a perfectly typical branch of *S. fluitans* (*III*) with its thinner, larger and more twisted leaves, its looser growth and more open foliation, dangling from an otherwise quite typical *S. fluitans* (*X*), with its dense globular growth of short, stiff branches, densely foliate with stiffer and less twisted leaves than those of *S. fluitans* (*III*), and closer examination of this stem of *S. fluitans* (*III*) reveals that it is actually a true branch from the clump of *S. fluitans* (*X*). An only moderately well developed example of this sort is shown in herbarium silhouette No. 37, fig. 20. Other examples in which the branch of *S. fluitans III* is larger and still more completely characteristic of this form, while the basal clump of *S. fluitans* (*X*) is also denser and more typical of its own kind are available in liquid preservation. In view of the scarcity with which these two forms of *S. fluitans* are thus found in organic continuity with each other, it is evident that when an *S. fluitans* (*III*) branch is formed it must break off very early and easily from the *S. fluitans* (*X*) clump. It also seems probable, in view of the generally 5–20 times greater amount of *S. fluitans* (*III*) found in the Sargasso Sea, that this form, once it has separated from *S. fluitans* (*X*), continues to grow and to multiply by fragmentation true to its own type.

If we consider the relationship between the long branches of *S. fluitans* (*III*) type and the short, crowded branches of *S. fluitans* (*X*) form in the plants in which both occur together, the situation obviously offers great similarities with the relationship between the long distal shoots and the ring of short basal branches so commonly observed in various forms of sessile *Sargassum*, particularly among the more robust species.

It therefore seems fairly reasonable to see a certain parallelism between the dimorphism of the pelagic *Sargassum fluitans* and the dimorphism between distal and basal shoots within a single specimen among the sessile species. If this parallelism is more than a figure of speech, it patently requires some explanation. While the writer is not able to suggest any definite theory bearing upon this problem, he feels that reference might be made to the fact that once the long distal branches have split off from the basal clump, the latter will, as it rolls around in the turbulent motions of the sea, only be able to maintain a radial orientation with reference to some point in its middle which becomes its average center of rotation; while the long distal branches (*S. fluitans* (*III*)) must tend to rotate around the *axes* of their main stems, and if they also have long lateral branches flattening out at the surface due to the buoyancy of their bladders, they should indeed tend to become relatively stable with reference to their position relative to the sea surface. If the ability to maintain a fairly steady axial orientation with reference to light, gravity, etc. favors growth of the *S. fluitans* (*III*) (distal shoot) type, and the complete lack of this ability favors the development of the basal shoot habitus of *S. fluitans* (*X*), we shall therefore be able to understand why either form tends to become self-perpetuating within its own type of growth after the plant has become pelagic and the two types of branches have become separated from each other by fragmentation.

Fertile Attached Specimen of *S. Fluitans*

A complete plant with fertile branches and a basal holdfast attached to what would appear to be a rather weathered piece of root (mangrove-root ?) was obtained in haul No. 133, on August 27–28, 1934, in average latitude 37° 50′ N. and longitude 69° 25′ W. The sterile parts of this plant fall completely within the usual range of variation in pelagic representatives of *S. fluitans*, with regard to all features of leaves, bladders, thorniness of stems, etc., even to the great paucity, irregularity, and inconspicuousness of the cryptostomata. The sterile branches, if collected separately, would therefore unhesitatingly have been referred to this species, and there is accordingly little reason to hesitate about identifying the entire plant in the same manner. It is, on the other hand, not possible to obtain an at all satisfactory agreement with any description of the currently recognized benthonic species of Sargassum from the Atlantic, and the name of *S. fluitans* Börgesen is therefore retained. While the general character of the plant points towards an affinity with the *Sargassum vulgare* group, the writer has, at least tentatively, come to the conclusion that this group in itself probably constitutes a very heterogeneous assembly of forms among which several taxonomically distinct units will probably become recognizable when more adequate collections are obtained. A diagnostic description of the specimen in hand follows:

Stems rather coarsely muriculate, with thorns extending on to the bases of some of the larger leaves and also occurring between the receptacles on a few of the ultimate receptacular branchlets. Leaves on ordinary branches, or on short spur branches of second or third order; subsessile, conspicuously assymetric at the base; fully developed leaves about 30–35 mm. long and about one-fifth as

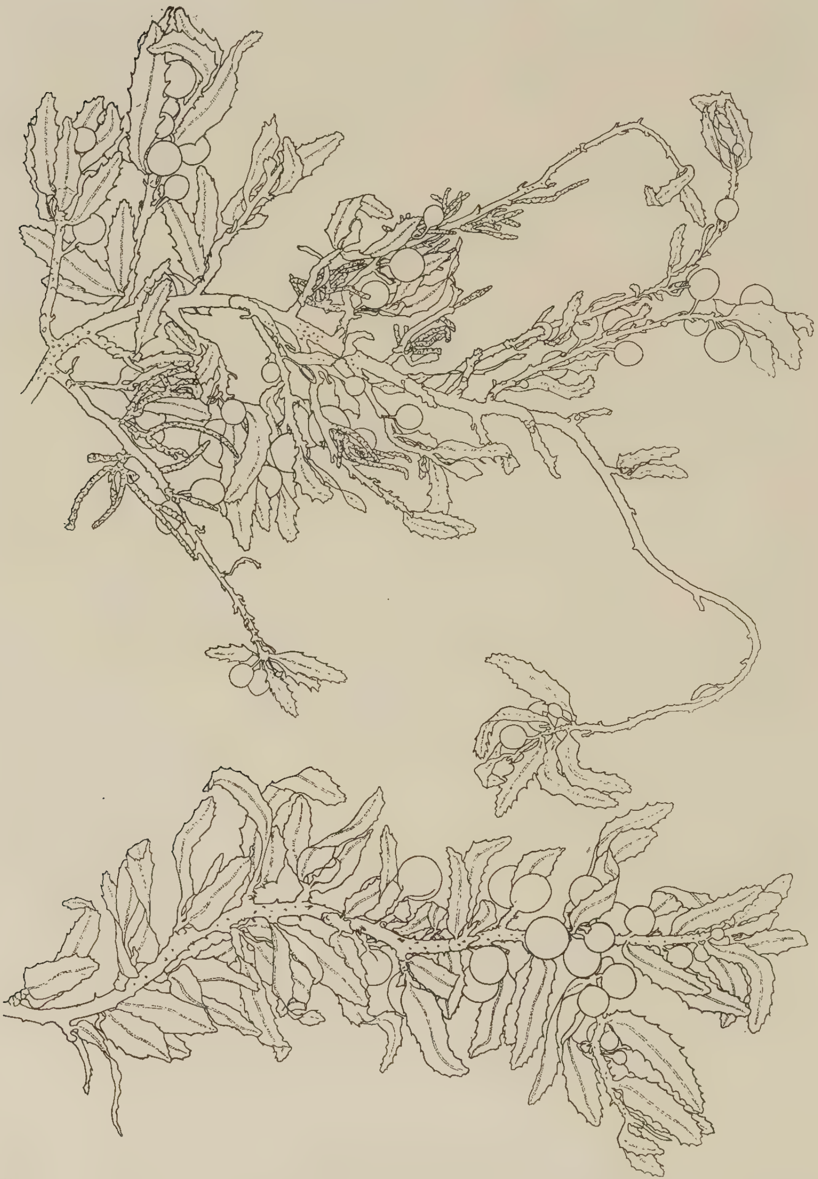


Figure 25. Specimen of *Sargassum fluitans* attached to drifting piece of wood. Fertile branch above, sterile branch below.

wide (6–7 mm.). Edges of leaves sharply serrate. Midrib distinct but without conspicuous ridge. Cryptostomata very small, few, inconspicuous and extremely irregularly arranged; entirely absent from many leaves. Leaves very crisp, moderately curled and twisted, fairly thick. Color yellowish brown. Receptacular branchlets long, irregularly branched, apparently not axillary,[1] sometimes with bladders and occasionally with very small leaves. Bladders up to 7 mm. diameter, entirely smooth, subglobular. Pedicels short, 1–3 mm., frequently coarsely muriculate, in one instance slightly dentate-alate. Holdfast almost encircles root to which it is attached, measuring 27 mm. in the longest direction. Two thick main stems arise from the holdfast, immediately dividing into numerous main branches so close to the base that they superficially appear as a cluster rising directly from the holdfast.

With this description and the accompanying illustration of parts of a complete plant of *S. fluitans*, it should be possible to give more definite direction to the further search for the benthonic sources from which the pelagic vegetation of this species may have been derived.

GENERAL QUANTITATIVE AND GEOGRAPHICAL RESULTS

In 1933 the first *Sargassum* collector was unfortunately lost by a parting of the towing wire after only a few hauls had been made south of Bermuda. On the remainder of the route to Nassau, Bahamas, where the collector was replaced, the passing weeds were sampled at random by long-handled dip-nets, giving a record of relative frequencies of the main species. Due to the pressure of hydrographic work, the operation of the *Sargassum* collector was later again abandoned *after the floating weeds disappeared* a short distance south of the Virgin Islands and was only resumed for a few hauls off the southern coast of Haiti, while observations from deck were, of course, made throughout the voyage, and isolated weeds were occasionally collected with a dip-net.

In 1934 and 1935 the operation of the *Sargassum* collector was continued for completeness of the record, also in waters where no weeds at all were obtained.

In the Gulf Stream region north of Cape Canaveral, Florida, weather conditions were generally found to be so unfavorable during the time of the cruises that only very little use (86.8 towing miles in two hauls, April 19–20, 1935) could be made of the regular collector after leaving Miami, Florida, on the return trip, but samples were taken by other means and observations were made from deck to the extent that the conditions would permit.

A complete account of the 194 hauls so far made is given in our tables on pages 85–90, using the designations explained in the preceding discussion of the taxonomy of the weeds.

---

[1] Unless there has been a consistent loss of associated branches or leaves.

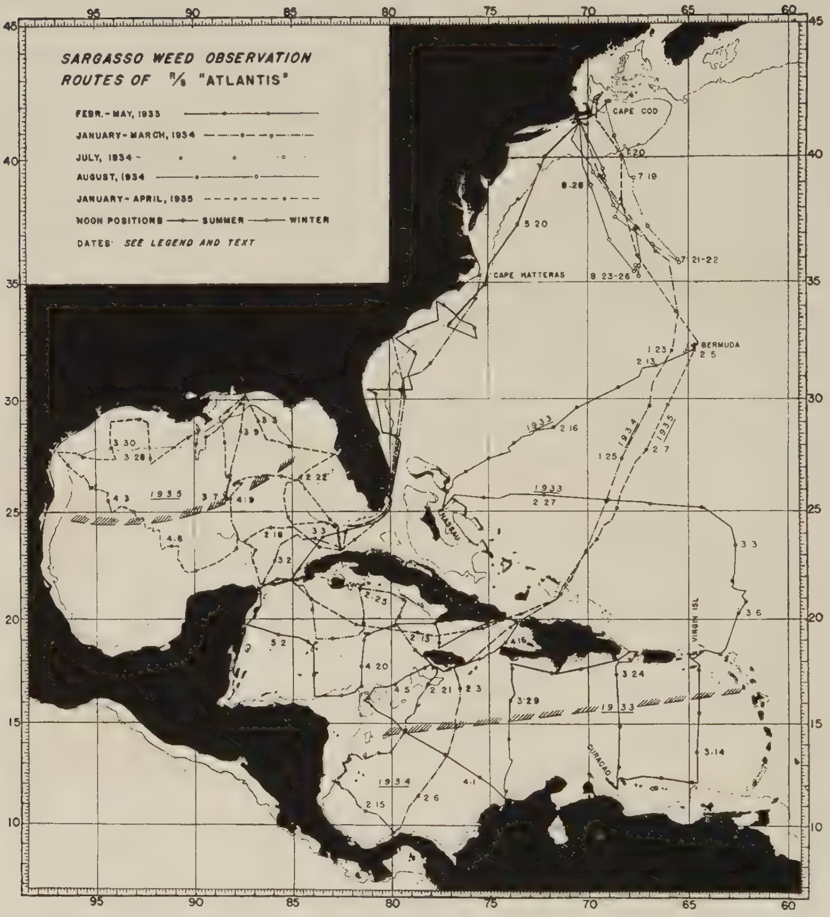

SARGASSO WEED OBSERVATION
ROUTES OF R/S "ATLANTIS"
FEBR.-MAY, 1933
JANUARY-MARCH, 1934
JULY, 1934
AUGUST, 1934
JANUARY-APRIL, 1935
NOON POSITIONS SUMMER WINTER
DATES: SEE LEGEND AND TEXT
CAPE COD
CAPE HATTERAS
BERMUDA
NASSAU
VIRGIN ISL.
CURACAO
1933
1934
1935
95
90
85
80
75
70
65
60
45
40
35
30
25
20
15
10

Figure 26. "Atlantis" routes over which Sargassum weed collections have been made. Dots mark noon positions with dates given at intervals (e. g. 3: 14 to be read: March 14).

DOMINANT FORMS

Among the eupelagic forms which altogether constitute more than 99 per cent of the total pelagic vegetation of the investigated portion of the Sargasso Sea proper, *Sargassum natans* (*I*) (*S. natans ciliata* Börgesen) and *S. fluitans* (*III*) far outweigh all other varieties in quantitative significance, comprising together between 89 and 99 per cent of the total. *S. fluitans* (*X*) and *S. natans* (*II*) (*S. natans typica* Börgesen) are next in importance in the order mentioned, the former occasionally, the latter only very rarely occurring even on the same order of magnitude of abundance in single hauls as the two varieties first named. Certain gross features of distribution would seem to be shared in common by all forms of the *S. fluitans* and *S. natans* series, except *S. natans* (*VIII*). These (see figure 26) consist of a common southern boundary of occurrence within the Caribbean along a line drawn from about 16°–17° northern latitude at the eastern end to about 14° in the west; in a very sharply marked change in abundance from the scarcity of the Caribbean region inside of the Antillean chain of islands to the relative richness of the Sargasso Sea proper outside; and in the occurrence of a secondary maximum in the inner portions of the Gulf of Mexico.

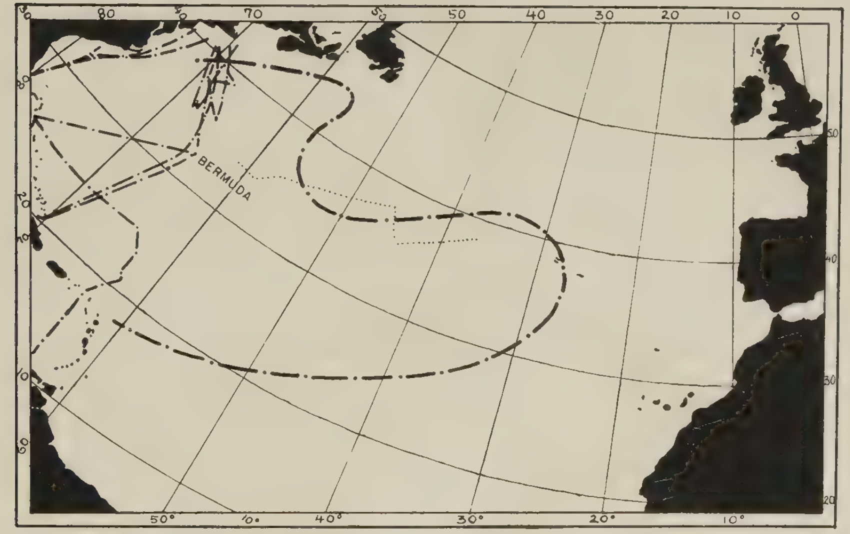


Figure 27. "Atlantis" routes (dot and dash) inserted in the contour line of the Sargasso Sea boundary drawn according to Winge (1923, Fig. 2). Dotted line indicates course over which weed was collected with dipnet by Mr. D. Spencer Berger during the summer of 1934.

Carribbean and Cayman Seas

The location of the southern boundary of significant occurrence of pelagic weeds within the Caribbean has been determined by visual observation over about 900 route miles on four crossings of the empty area in 1933 (see figure 26), and by 648.6 towing miles with net empty[1] of eupelagic weeds (except *S. natans* (*VIII*)) over about 800 route miles in 1934.

[1] Within the first 100 miles south of the boundary marked on figure 26 isolated small sprigs of eupelagic weeds too scarce for quantitative measurements are occasionally obtained, but still farther south even such rare fragments are totally absent from all hauls (except *S. natans* (*VIII*)). That scattered weeds must occasionally spread beyond the normal boundary of pelagic vegetation is of course obvious.

Between this southern boundary of weed occurrence and the Yucatan Channel the Caribbean area includes about 375,000 square nautical miles.

The failure of the pelagic vegetation to penetrate southward into the Caribbean Sea is in excellent agreement with the findings of Nielsen (1925) and of Parr (1937, p. 85), showing that the surface water of the Caribbean is mainly or entirely of southeastern origin, while the Sargasso Sea water only penetrates into the Central American basins at intermediate depths in the maximum salinity layer.

The change in abundance of pelagic weeds per mile from the Sargasso Sea proper to the Caribbean, which occurs abruptly at the various passages between the Antillean Islands, is not a mere matter of differences in precise amounts but one of differences in the order of magnitude of weed abundance, the average quantities per mile found inside of the Caribbean region north of the southern boundary of weed distribution (91.7 towing miles in 1933; 911.6 towing miles in 1934; 540.7 towing miles in 1935) being for both of the dominant pelagic forms (*S. natans* (*I*) and *S. fluitans* (*III*)) less than one-tenth of the averages obtained in the Sargasso Sea proper (see table on page 59). From the records for 1934 it would appear that the relative difference between Caribbean and Sargasso Sea abundance in that year at least was even much greater in the case of *S. natans* (*I*) (ratio 50 : 1) than in the case of *S. fluitans* (*III*) (ratio about 15 : 1). The explanation of this geographical difference in *relative* distributions of the 2 species in 1934 is not clear, but it is evident from our observations of the great variations in local abundance over short distances within the Sargasso Sea proper, as shown by the fluctuations in pounds per mile in successive hauls, that chance distribution of the pelagic weeds in the regions near the various entrances to the Caribbean, and chance variations in winds and currents as well, must play a very important part in the quantitative relationship between Caribbean and Sargasso Sea vegetation, and that this relationship can therefore not be expected to show any great degree of constancy from time to time.

The pelagic weeds of the Caribbean and Cayman Seas are generally fresh, healthy and vigorous looking, with no evidence of significant mortality anywhere. Nor do epizoan incrustations, although on the average somewhat more abundant than in the Sargasso Sea, ever seem to reach an intensity which would constitute a threat to the buoyancy and the survival of the weeds.

Gulf of Mexico

In the secondary region of abundance in the inner portions of the Gulf of Mexico (see figure 26) the quantities of weeds per mile (696.9 towing miles, March–April, 1935) reach or approach the order of magnitude of the quantities observed in the Sargasso Sea proper, without reaching quite to the same average amounts. As we may see from the table on page 59 *S. natans* (*I*) accounts for 87 per cent of the eupelagic weeds, and among the remaining 13 per cent, *S. natans* (*VIII*) and *S. fluitans* occur in about equal quantities. Holobenthonic weeds are surprisingly rare in comparison with their occurrence in the Caribbean and the Straits of Florida in similar semi-neritic waters, being far too scarce for quantitative recording.

As shown on our map the secondary region of abundance includes about 90 thousand square nautical miles; with an average of about 1 ton per square mile (see table, p. 59) its total floating vegetation at the time of observation may therefore be estimated in rough approximation at about 90,000 tons wet weight.

That there should be an accumulation of floating weeds in the inner portions of the Gulf is natural to expect when we remember that the transportation of these plants must be as much, if not more, influenced by winds as by ocean currents, and that the winds over the Gulf of Mexico and adjacent waters have a prevailing easterly component at all times of the year. There would thus be a general tendency for weeds floating in through the Yucatan Channel to be driven into the Gulf in a westerly or northwesterly direction, and to accumulate there in the northwesterly portion, even though the waters of the Caribbean current turn sharply to the right and flow directly out through the Straits of Florida (Parr 1935).

The secondary maximum in the Gulf of Mexico is entirely separated from the Sargasso Sea proper without any continuity of abundance through the intervening region (660.8 towing miles in the southwestern part of the Gulf and in the Straits of Florida, April 1935). This complete segregation of the two communities of abundant pelagic vegetation is further confirmed by other evidence from the character of the weeds themselves and their epizoan fauna, as we shall immediately see.

Compared with the vegetation of the Caribbean and the Sargasso Sea proper, the eupelagic weeds of the secondary maximum in the Gulf of Mexico were, at least at the time of sampling (March–April, 1935), of a relatively unhealthy appearance throughout. Of the three varieties above mentioned, *S. fluitans* shows the effects of the presumably adverse conditions in the Gulf even more strongly and more generally than the other two, being present chiefly in the form of small, chopped fragments of only a few inches length, while complete plants are relatively very scarce. In the case of *S. natans* (*VIII*) larger plants are much more frequent than in *S. fluitans*, but small fragments also abound, and a majority of the larger pieces bear evidence of a more or less extensive loss of leaves, bladders and branches. Of the three eupelagic forms *S. natans* (*I*) may perhaps appear to be the variety most, or longest, able to withstand the adverse circumstances, although this distinction is very difficult to draw. Except in the northwestern boundary zone, this form is usually comparatively fresh in its most distal portions, while the proximal parts generally show strong evidence of degeneration and decay to an extent only rarely seen in other waters. The prevailing size of plant also differs less from the normal in the case of *S. natans* (*I*) than in the case of the other two varieties just discussed.

Towards the northwestern boundary of the secondary maximum, however, all three varieties seem to reach an apparently dying state together in which *S. natans* (*I*) also breaks up, loses the remnants of its distal freshness, and suffers extensive losses of leaves and bladders along with the other two forms. It may be mentioned at this point that perhaps due to mechanical rather than physiological strength, the largest and least mutilated pieces found at the extreme northwestern boundary generally belong to *S. natans* (*VIII*).

Parallel with the deterioration of the plant itself, we find a greatly increased epizoan infestation of the floating weeds in the secondary maximum, unequalled anywhere else except in isolated instances. This infestation also reaches a maximum at the northwestern boundary particularly in regard to heavy incrustations by such forms as *Membranipora* and it is evident that the weight of these incrustations here very frequently must cause the plants or plant fragments to sink from the surface and may perhaps occasionally do so throughout the secondary maximum, contrary to what we have found in the Caribbean and the Sargasso Sea proper.

Taken all together the features of the pelagic vegetation in the secondary maximum are so distinct that a random sample could never be mistaken for a sample from any other region studied in the course of these investigations. Geographically the occurrence of vegetation of this type is sharply limited to the inner portion of the Gulf of Mexico with no evidence of a dispersal towards the southeastern region of the Straits from which it might spread to other waters via the Florida current and the Caribbean counter-current following the Yucatan coast to the southward.

The complete segregation of the secondary maximum is moreover suggested by Burkenroad's findings that the epizoan communities associated with the weeds of the secondary maximum are to some extent different from those of any other region, both in their composition in regard to dominant forms and by the presence of various endemic species, including even a separate species of *Sargassum* crab (*Portunus*).

This segregation also confirms the author's earlier conclusion from hydrographic data (Parr, 1935) that there is no significant outward flow of the surface waters from the inner Gulf of Mexico to the Straits of Florida (at least during the winter season). If such outflow did occur at a significant rate with reference to the accumulation of floating weeds, every period of calm (or absence of easterly winds) would see a dispersal towards the Straits of Florida, and it would scarcely be conceivable that such a well-defined maximum could accumulate and maintain its position, if its existence were based upon a precarious balance in a conflict between direct wind drift to the northwest and an underlying permanent tendency for steady currents in the opposite direction.

It is evident from the foregoing that the secondary maximum in the Gulf of Mexico can hardly represent an essentially self-sustaining unit of vegetation similar to that of the Sargasso Sea proper (see pp. 68–84), but is rather to be regarded as a comparatively stagnant accumulation of slowly perishing weeds deflected from the surface drift of the Caribbean current on its passage from the Yucatan Channel to the Straits of Florida (see Parr, 1935). A relatively high mortality is apparent from the character of the weeds themselves, particularly in the northwestern portion of the maximum during the period of sampling, and can further be deduced from the fact that the strict confinement of the weeds and their characteristic epizoan fauna to the inner portions of the Gulf clearly shows that this secondary maximum of pelagic vegetation has no significant outlet to adjacent regions and that its mortality must therefore on the average compensate for the additions received from Caribbean waters.

It should be mentioned at this point that *S. natans* (*I*), constituting as we have seen more than 85 per cent of the floating weeds of the secondary maximum, shows no more morphological evidence of recent derivation from the bottom in this region than it does in the middle of the Sargasso Sea proper. On the contrary, it does as a rule, when reasonably well preserved with fresh distal portions, show an even more general lack of plane or axial orientation (see page 46) than the average in the Sargasso Sea, being usually of a quite regularly globular habitus. On general appearance one would therefore without much hesitation or doubt judge it to be an old pelagic weed, and the author is quite confident that the possibility of significant local sources may be completely disregarded. In regard to the other two relatively insignificant weeds, it is more difficult to have a definite opinion on this point, partly due to their poor condition in the secondary maximum (*S. fluitans*) and partly for other reasons connected with their general distribution.

Although we have thus come to consider the secondary maximum as a chance aggregation of moribund plants, the fact that an accumulation does occur and that a special epizoan fauna can develop in connection with it and can reach an abundance not seen elsewhere, clearly shows that the process of destruction must even here require on the average a very considerable time. How long must for the present remain an open question.

That the presumably high mortality of weeds in the secondary maximum will probably not be equally distributed over all seasons of the year goes without saying. Undoubtedly the mortality must reach its maximum during the period of minimum temperatures (air and water, see page 81–82) and must then in all probability be even greater than indicated in our material which was all collected after the spring equinox (apart only from a few samples in the presumably healthier southeast corner of the secondary maximum).

Although the loss by mortality (including sinking of overloaded living plants) must be sufficiently in excess of growth increment to balance the addition of drifting plants from the Caribbean, since otherwise the accumulation would become infinite, there is nevertheless every indication in the appearance of the apical points of the weeds in better condition that some slight growth may have been occurring even at the time of sampling, and this growth should be expected to increase during the warm season. It must, on the other hand, probably be during the relatively unproductive winter months with their high mortality that the pelagic vegetation makes its greatest contribution to the layers below. The quantitative importance of the pelagic Sargassa in the total metabolism of the sea must, however, be quite as insignificant in the Gulf of Mexico as in the Sargasso Sea proper for the reasons explained on pages 67–68.

It is probable that the secondary maximum in the Gulf of Mexico may change its location from time to time according to changes in meteorological and hydrographic conditions, but it might be worth mentioning that the Gulf of Campeche, i. e., the southwestern part of the Gulf of Mexico west of the Campeche Bank was found to be free of floating weeds also when visited by the Mabel Taylor expedition in April, 1932.

Sargasso Sea

Figures 28 and 29 shows the poundage per mile of *Sargassum fluitans* (*III*) and *S. natans* (*I*) in the Sargasso Sea proper, i. e. in the region between Bermuda and the Antilles, plotted against the distances traveled, and the length of the individual hauls represented by the width of each column. By the ratio between the blank distances and the distances covered by the black histograms the figures thus also give an impression of the extent to which the region has been sampled with the collector actually operating in the surface. The total towing mileage within the Sargasso Sea proper (south of Bermuda) adds up to 1316 nautical miles distributed on the individual years in the following manner: *1933:* 268 miles; *1934:* 526 miles; *1935:* 522 miles. From these hauls a total of 3090 pounds of pelagic weeds (*1933:* 689.5 pounds; *1934:* 1635.5 pounds; *1935:* 765.5 pounds) were obtained, weighed, sorted and examined.

From the records for 1934 it looked as though there might be a center of abundance of floating weeds in the approximate geographical center of the area investigated, but the figures obtained in 1935 show this feature of distribution to have been only of a transitory character subject to very great changes with time. It is quite evident from our figures that it would be absolutely impossible from the data for 1934 and 1935 combined to attempt to determine zones of various degrees of abundance within the Sargasso Sea proper; but this may in itself be regarded as a very useful and important addition to our knowledge of the pelagic vegetation, since it shows very clearly an extremely high degree of variability in the distribution of weeds from time to time, and enables us to avoid premature conclusions on the assumption of more stable conditions. Considering the scale on which the sampling was undertaken, a discussion of zones of abundance might reasonably have been considered justified on the basis of the data from 1934, in the absence of the records for 1935. As it is, such detailed considerations will have to be postponed until we can begin to work with averages of observations many times repeated over the same routes. At the present stage we must confine ourselves to a discussion of the gross averages for each year over the entire length of the routes falling with the Sargasso Sea proper. These averages distribute themselves in the manner shown in the table given on the next page.

In the region of the Western Sargasso Sea north of 35° northern latitude (see figure 30, p. 62) we are in the marginal zone of the pelagic weed community. Seasonal fluctuations in the location of the northern limits of survival and other variable factors of the environment in this region obviously make it unwise to attempt any generalizations and computations of averages until much more information may become available than that which is now at hand. The records from this northwestern area are therefore simply presented without further comment in the route-histograms given in figure 30.

AVERAGE AMOUNTS OF EUPELAGIC WEEDS ESTIMATED
IN KILOGRAMS PER SQUARE NAUTICAL MILE

	Nassau to Virgin Is.	Bermuda to Turks Is.	
SARGASSO SEA:	1933	1934	1935
S. natans(*I*)	2,019	4,863	1,117
S. fluitans (*III*)	1,445	458	652
All others	85	46	228
Totals, Sargasso Sea:	3,549	5,367	1,997
NORTHERN CARIBBEAN:	1933	1934	
S. natans (*I*)	68	94	
S. fluitans (*III*)	46	30	
All others	—	3	
Totals, Caribbean:	114	127	
CAYMAN SEA:			1935
S. natans (*I*)			24
S. natans (*VIII*)			11
S. fluitans			36
Total, Cayman Sea:			71
SECONDARY MAXIMUM, GULF OF MEXICO:			1935
S. natans (*I*)			884
S. natans (*VIII*)			66
S. fluitans			67
Total, Secondary Maximum:			1,017

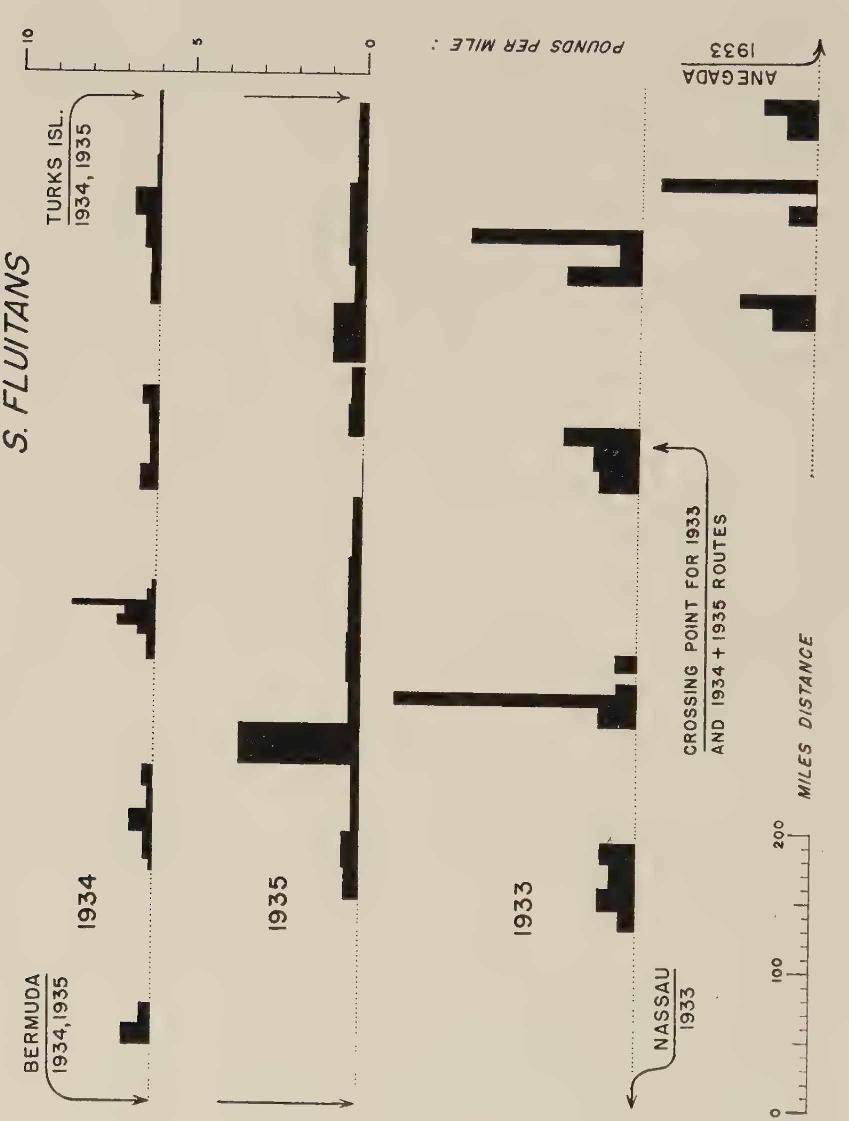

S. FLUITANS
POUNDS PER MILE :
10
5
0
TURKS ISL.
1934, 1935
BERMUDA
1934,1935
1934
1935
1933
NASSAU
1933
ANEGADA
1933
CROSSING POINT FOR 1933
AND 1934 + 1935 ROUTES
MILES DISTANCE
0
100
200

Figure 28. Route histograms showing abundance of *Sargassum fluitans* (*III*) in the Sargasso Sea. See legend of figure 29. Note that scale of pounds per nautical mile is five times as large as that used in figure 29.

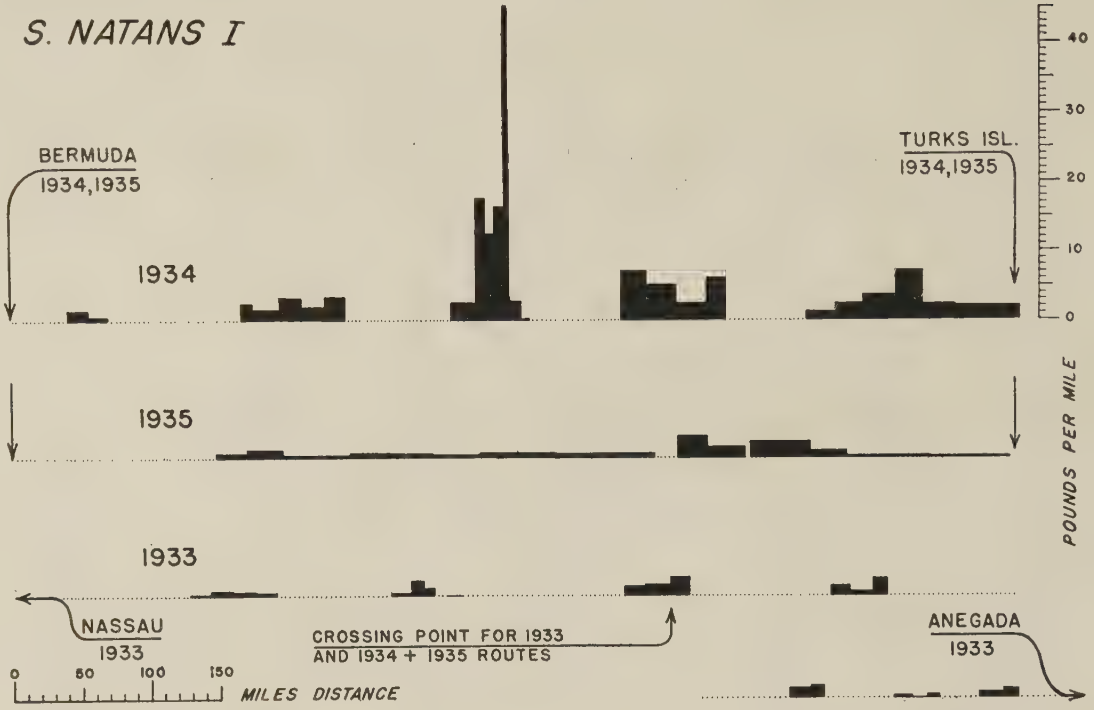


Figure 29. Route histograms for *Sargassum natans* (*I*). Quantity in pounds per nautical mile shown by the heights, length and location of the hauls by the widths and positions of the columns. The 1934 and 1935 routes are virtually identical, while the 1933 route crosses their tracks nearly at right angles at the point shown by arrow. See figure 26.

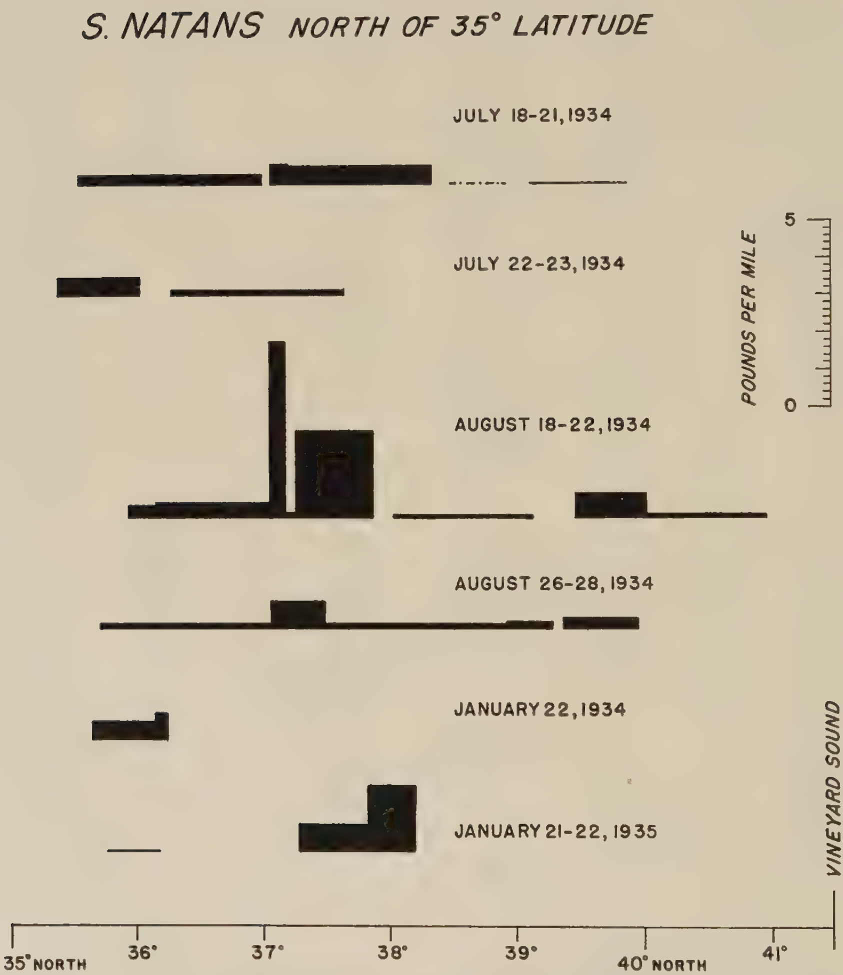


Figure 30. Route histograms indicating the abundance of *Sargassum natans* (*I*) at various times of observation north of 35° northern latitude. Base of histograms measured by latitude instead of route miles.

ANNUAL FLUCTUATIONS

From the table on page 59 we see that the variations observed from year to year are not merely variations in distribution but also variations in the ratio of almost 1 : 3 in the total abundance of weeds over the routes traveled, which were virtually identical in 1934 and 1935. The greatest ratio of variation (almost 1 : 5) is observed in the quantities of *S. natans* (*I*), although this remains by far the most abundant weed in all three years. That these annual variations do not merely appear fortuitously in our records due to inadequate sampling but actually express a real difference in the abundance of pelagic weeds between January 1934 and February 1935 may safely be taken for granted when we consider that the cumulative towing mileage in each year covered a little more than two-thirds of the total distance between Bermuda and Windward Passage. There is, according to the statements of the guard at Fort St. Catherine beach,

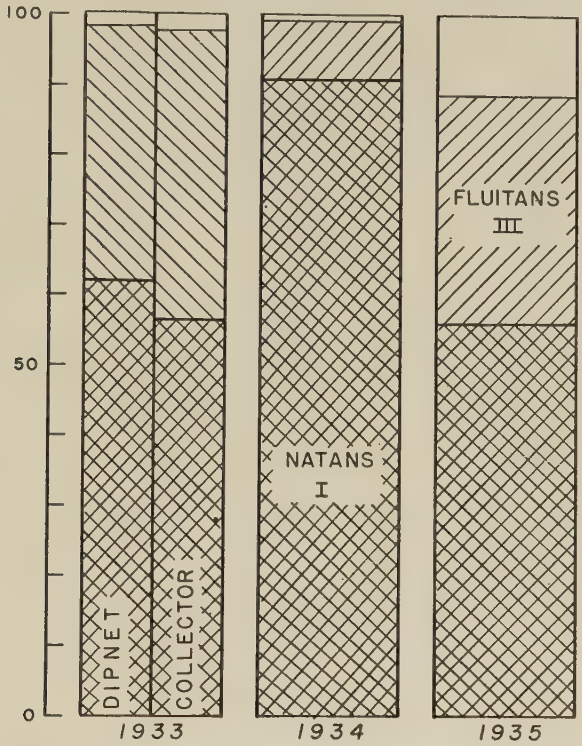


Figure 31. Variations in average relative abundance by weight of *Sargassum natans* (*I*) and *Sargassum fluitans* (*III*) in the Sargasso Sea, south of Bermuda, in 1933, 1934, and 1935.

also corroborative evidence for this conclusion in the fact that much less weed drifted into the beaches of Bermuda in 1935 than in 1934, as judged by the amount of work required to keep the beaches clean during these two years.

So long as no quantitative data are available from other parts of the Sargasso Sea, it is, of course, an open question whether this difference in abundance over the Bermuda-Windward Passage route expresses an annual difference in the total amount of pelagic vegetation in the entire domain of the drifting weeds, or merely indicates a change in their distribution, the centre of abundance being located farther to the eastward in 1935. There is, however, in the author's opinion, no *a priori* reason to assume that such annual changes in abundance might not affect the total vegetation of the entire Sargasso Sea, the combination of growth conditions and loss in the marginal zones being more favorable in some years than in others.

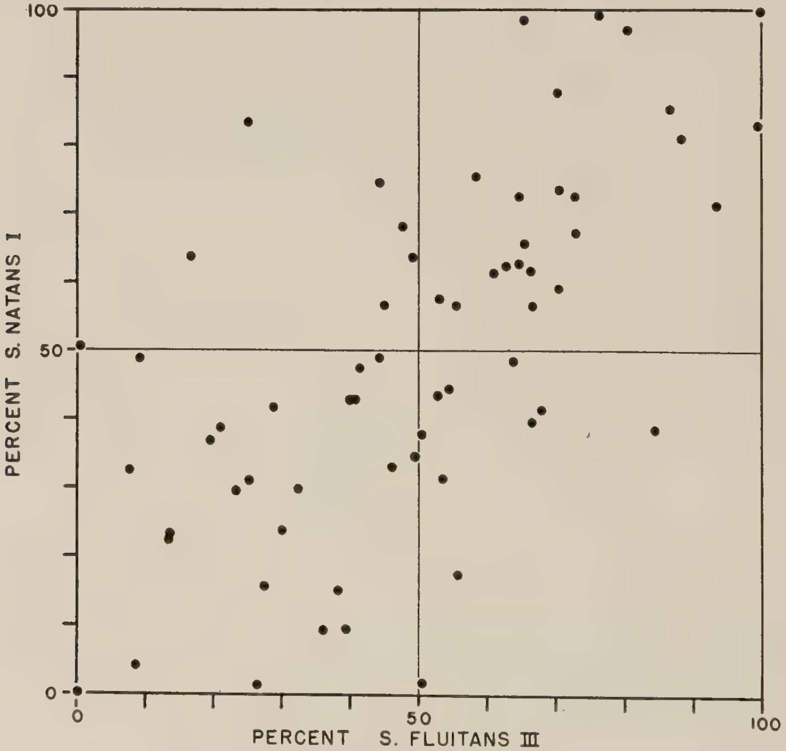


Figure 32. Correlated variations in amount of *Sargassum natans* (*I*) and *S. fluitans* (*III*) on successive hauls. Amount per haul expressed in per cent of the sum of the quantities obtained of each species in the haul considered and in the haul immediately preceding. See text.

CORRELATED VARIATIONS IN WEED DISTRIBUTION

It is perhaps a purely fortuitous circumstance that the year of maximum abundance of *S. natans* (*I*) is the year of minimum abundance of the other pelagic forms over the routes traveled. On this point a comparison might also be made with the relative quantities obtained on the route from Bermuda to Nassau, Bahamas, by random sampling with a dip net (see page 51).

Frequencies of Pelagic Weeds in Per Cent of Total

	1933		1934	1935
	Nassau to Virgin Isl.	Bermuda to Nassau	Bermuda to Turks Isl.	
S. natans (*I*)	56.3%	62.0%	90.7%	55.9%
S. fluitans (*III*)	41.3%	36.4%	8.2%	32.6%
All others	2.4%	1.6%	.9%	11.4%

If we consider the variations in the amounts of the different weeds obtained in the single hauls, we generally find a very definite positive correlation between the quantities of *S. natans* (*I*) and *S. fluitans* (*III*), showing that these forms, as were to be expected, follow the same general laws of local dispersal or aggregation under the influence of winds and currents and do not normally show any tendency to alternate in their occurrence over short distances. This positive correlation in the variations of single catches is shown in our figure 33 where the amount per haul of the two varieties above mentioned is expressed in per cent of the sum of the quantity in the haul considered and that in the preceding haul so that values from 50% to 100% express an increase, and values below 50% a decrease from the preceding catch. This positive correlation between the variations in the quantities of the two species in succeeding single catches refers only, of course, to local variations in distribution and has absolutely no direct bearing upon the problem of possible fundamental differences in their distribution of abundance over larger areas or in point of longer time intervals.

DISTRIBUTION OF LESS ABUNDANT FORMS

In view of the great predominance of *S. natans* (*I*) and *S. fluitans* (*III*) in the pelagic material the preceding discussion of the general quantitative distribution of floating weeds also constitutes a specific discussion of the distribution of these two forms. For the less abundant varieties the quantitative data are not adequate for a discussion of distributions in numerical terms.

In general, *S. natans* (*II*) and *S. fluitans* (*X*) show the same distribution pattern as *S. natans* (*I*) and *S. fluitans* (*III*), being most frequent where the latter are most abundant.

S. natans (*IX*) can, on the other hand, almost be described as endemic of the Cayman Sea east of the main Caribbean current, where it may even exceed the typical *S. natans* (*I*) in single hauls (No. 162). *S. natans* (*IX*) is also occasionally seen downstream as far as the Straits of Florida, but we have no specimens which we would refer to this form from any region beyond the Straits. Its morphological intergradations with the *S. natans* (*I–II–VIII*) series would make it seem very unreasonable to regard *S. natans* (*IX*) as anything but a phenotypic modification. In its typical, and predominant form, it can nevertheless be quite as easily differentiated from the other forms of the *S. natans* series as these can be differentiated among themselves, and it seems somewhat surprising to find such a distinct variety with so limited distribution. Since such specimens can obviously not change their appearance very rapidly, and since, moreover, *S. natans* (*IX*) is characterized by a greater relative abundance of bladders than that observed in the other forms, which would prevent it from sinking at a more rapid rate than these, it seems implied that the absorption of surface drift from the eastern Cayman Sea into the main Caribbean current must be rather slight.

The distribution of *S. natans* (*VIII*) is in various essential features entirely different from that of *S. natans* (*I*), *S. fluitans* (*III*) and all the other pelagic forms. Although *S. natans* (*VIII*) occurs with the others also in the open Sargasso Sea, it is definitely rare in that region, and has its main distribution *within* the Central American seas where the other forms occur only secondarily and in lesser abundance than in the Atlantic. We have mentioned already that, although rare, as are all pelagic weeds, south of the southern boundary of normal occurrence in the Caribbean, *S. natans* (*VIII*) constitutes the *majority* of the scattered sprigs occasionally encountered in southern Caribbean waters, while it is in very rare minority in the Atlantic. In one instance 1.2 pounds of this form were collected in the S-W bight of the Caribbean near the southern end of Mesquito Bank, with no other pelagic weeds but with four pounds of benthonic weeds present. *The S. natans VIII* flora is thus the only one which would be capable of entering the Caribbean Current from the left, while *S. fluitans* and *S. natans I–II* impinge upon its flow from the right-hand side. In the Northeastern Cayman Sea *S. natans* (*VIII*) is quite common and the 1935 records show a couple of hauls between Cuba and the Cayman Islands in which this was the most abundant form, although the weight per mile did not exceed 1/30 of a pound. In the Gulf of Mexico *S. natans* (*VIII*) reaches its greatest absolute abundance, frequently exceeding one-tenth of a pound per mile (1935), but the secondary maximum, with reference particularly to the distribution of *S. natans* (*I*) in this region, causes the indicated relative abundance of *S. natans* (*VIII*) to be less in the Gulf than in the Cayman Sea. If it should otherwise prove possible and reasonable to attempt to derive the *S. natans* series from a broad-leaved, rather than a narrow-leaved, benthonic relative via *S. natans* (*VIII*), the geographical distribution of this form with its maximum abundance within the Central American seas instead of in the open Atlantic, would lend support to this interpretation to which the author is also otherwise inclined.

The peculiar dwarf form, Winge's *Sargassum V*, seems generally distributed in the western Sargasso Sea and also occurs in Central American waters, but is everywhere so scarce that no discussion of relative variations in abundance seems possible. Our material entirely confirms Winge's observations on the peculiarly high frequency of this otherwise scarce weed in the bundles of floating *Sargassum* of which the flying fish form their nests.

TOTAL QUANTITY OF PELAGIC VEGETATION

In spite of the great differences in the average quantities obtained from year to year, it will be seen from our table on page 59 that all our records for the Sargasso Sea proper remain within the same order of magnitude and it is probably safe to assume that this therefore expresses at least the order of magnitude of the abundance of pelagic weeds for the entire Sargasso Sea. As outlined by Krümmel and by Winge, the region of the Sargasso Sea includes about two million square miles. From our table on page 59, we see that the total quantity of floating weeds per square mile is to be reckoned in tons, the total vegetation of the entire Sargasso Sea must therefore be on the order of magnitude of millions of tons. Specifically our records for the various years applied to the entire region would give a total estimate of about 4 million tons on the basis of the 1935 data, 7 million tons on the basis of the 1933 observations, and 11 million tons according to the records of 1934. Other things being equal it is, of course, most likely that the true value should be within the range of those above estimated, and until further data become available, we may accept this probability with proper reservation as a working hypothesis. Regardless of the still very tentative character of this assumption as to the limitations within which the exact value is likely to fall, there is no valid reason to doubt that at least the correct order of magnitude is indicated in our figures as already above mentioned and to that extent we shall in the following discussions consider them valid without further reservations.

A floating vegetation of millions of tons of pelagic *Sargassum* seems very impressive at first thought, and has already tempted such eminent investigators as Hjort (in Murray and Hjort, 1912, p. 718) to refer to the presence of these floating weeds at the surface in explanation of an increased abundance of animal life at the deeper levels of the Sargasso Sea. But a comparison with the estimates of total oceanic productivity now available immediately shows that the drifting Sargassa can only be a quantitatively very insignificant element in the general metabolism of the sea, even within the region of their maximum abundance.

Atkins (1923) and Cooper (1933, 1934) have calculated the total annual phytoplankton production in the British Channel to be around 1.4 kilograms wet weight per square meter of surface, corresponding to nearly 5000 tons per square nautical mile, and Seiwell (1935) has given reasons for assuming that the productivity of the tropical North Atlantic must be at least on the same general order of magnitude as that of more northern waters. Comparing with our own observations of average abundance of pelagic *Sargassum* (2–5½ tons per square nautical mile) we thus find that the standing crop of floating vegetation even within the Sargasso Sea proper is only on the order of magnitude of thousandths of the probable total annual (plant) production of these waters. While we do not have any definite information as yet as to the actual rate of growth of pelagic *Sargassum*, it is undoubtedly safe to assume that they do not produce in excess of ten times their own weight per year, and it seems most likely that their actual growth will only be a fraction of this amount. Taking a ten times turnover as our maximum figure, we see that the floating vegetation will, at a very liberal maximum, only be able to account for hundredths or less of the probable total annual production of the Sargasso Sea.

DURATION AND NATURE OF THE PELAGIC PHASE OF THE FLOATING SARGASSA

One of the most debated questions in marine biology is the problem of whether the population of floating weeds occupying the so-called "Sargasso Sea" is merely a chance aggregation of slowly perishing individuals unable to maintain a prolonged existence when torn away from their "normal" benthonic habitat, or whether it is an essentially self-sustaining community of plants to which the pelagic existence has become secondarily normal, and which are able to maintain and multiply themselves indefinitely by mere vegetative growth, mechanical fragmentation, and irregular partition of the individuals through disintegration from the basal end.

Reviewing the history of the problem it is perhaps fair to say that the more direct the method of approach and the more adequate and accurate the material and observations, the more definite have the various investigators been in their acceptance of the latter theory, while the opposing viewpoint has been mainly based upon circumstantial and indirect reasoning with frequent resort to unsubstantiated specific assumptions from general knowledge.

In Winge's report the various arguments for or against the theory of an essentially self-sustained pelagic *Sargassum* population have been so fully set forth and critically analyzed that no detailed account of the entire discussion is necessary at this time, and we shall therefore merely confine ourselves to a brief restatement of the main points brought out by previous workers, in so far as they have withstood criticism and remain to be considered today.

In favor of the theory of an enduring pelagic existence the following three arguments already advanced in the previous literature would seem to have the greatest significance.

1) It was calculated by Krümmel (1891, p. 140) that it would on the average take the benthonic weeds detached from the shores of the Bahaman region at least about half a year (5¾ months) to drift around to the eastern part of the Sargasso Sea (that the possibility of eastern sources of weeds derived from the bottom is without quantitative significance has long been recognized) and a much longer time would of course be required for them to be spread over the entire oceanic domain of the pelagic *Sargassum.* Krümmel accordingly postulates that the weeds must at least be able to endure a pelagic existence for several years since their oceanic distribution otherwise becomes quite inexplicable. It is difficult to see how any valid objections might be raised against this argument, and its general import has also been accepted by Winge (1923). On this point one may also now claim definite support from the results of the Danish eel investigations[1] which show that the pelagic larvae of the European eels, hatched in the southwestern part of the Sargasso Sea, take 2–2½ years to reach the coastal waters of Europe, towards which they are being carried by the North Atlantic Current system which is also responsible for the distribution of the pelagic *Sargassum.*

2) Although direct observational evidence is as yet lacking, the vigorous appearance of the entire vegetation in the central area of the Sargasso Sea speaks very convincingly of plants in active growth, a fact which was first commented upon by von Humboldt,[2] and has been repeatedly confirmed by independent observations of numerous later investigators,[3] most recently by Ostenfeld, who states (in Winge 1923, p. 19) that "there is no doubt that *Sargassum*-shoots grow rapidly while drifting." Disregarding the problematical question of the *speed* of growth, which can be definitely settled only by direct experimental observations, the present writer entirely fails to see how any doubts could ever be entertained in regard to the universal occurrence of growth as such by anybody who has had opportunity to observe the living, pelagic weeds at sea, with the healthily-colored budding leaves, branches and vesicles on their distal portions and their vigorous older parts.

3) From Krümmel's and Antze's figures Winge (1923, pp. 17 and 20) has also claimed to be able to extract definite statistical evidence of growth among the pelagic weeds by showing that their frequency is subject to a simultaneous increase in all regions of the Sargasso Sea from summer to fall, a phenomenon which would be inexplicable on the assumption that all increases of the floating population must be due to the detachment of new contingents of weeds from benthonic fields, since these, in so far as they exist, can only be located along the Western boundaries of the Sargasso Sea. While fully accepting the fact of pelagic growth, as already above mentioned, the author is inclined to look for a modified interpretation of the change in statistical frequency pointed out by Winge. When dealing with frequencies one must always keep in mind that a frequency is only a purely numerical index without quantitative significance in terms of weights or volumes (see page 2). The fact that the recorded frequency of weeds is increased from summer to fall therefore merely means that a greater number of individual observations of floating vegetation have been made in the fall, but does not necessarily imply that the greatest increase in the total bulk of the population has occurred during this period. It is undoubtedly reasonable to assume, as Winge does, that the warm season must be the most propitious season for pelagic *Sargassum* growth. As it happens, the warm season is also generally the calmest season in the Sargasso Sea. From spring to early fall the weeds will therefore not only have their best growth, but will also perform this growth with relatively little partition of the plants, and the increase in bulk will therefore not be fully reflected in a corresponding increase in frequency. At the onset of the stormier season, the individual plants should therefore be expected to be of the greatest average size and therefore most likely to break down under the force of external disturbances which are undoubtedly a major factor in the process of their partition. Once the breakdown has occurred the resistance of the now smaller plants to further disrupting influences has thereby been increased so that continued disturbances will only have a greatly reduced effect upon their multiplication by fragmentation, in comparison with the effectiveness of the first onset of the disturbances in the fall. Following this period of maximum multiplication in the fall we can then safely assume that there must be a period of maximum loss of entire plants during the cold season when the marginal danger-zone of low temperatures along the entire northern boundary (see page 81) advances into the territory of previously favorable conditions, at the same time as the increasing strength of the easterly trade winds at lower latitudes must cause an increased amount of pelagic weeds to be thrown ashore on the Antillean and Bahaman coasts in the South-West. Within the statistical pattern of a self-sustained pelagic vegetation, growing slowly in bulk throughout the warm season, it is therefore possible to expect a relatively sudden increase in frequency, i. e., in number of plants in the fall, followed by a slow decline both in frequency and bulk during the winter, and with the decline in *frequency* quite likely to continue through the season of active increase in total bulk, in the absence of adequate external disturbances to cause the mechanical multiplication of the growing plants, while loss of entire plants in the marginal zones goes on all year round to a greater or less extent. With full recognition of these possibilities, however, the author is strongly inclined to doubt that even they are sufficient to explain the annual cycle in the frequency with which drifting weeds are encountered by passing ships, particularly on the point last mentioned in the preceding, i. e. with regard to the surprisingly high rate at which the decline in the frequency of the weeds is continued up to midsummer, as shown by the following relative frequencies for the entire Sargasso Sea taken from Winge (1923, p. 16).[1]

---

[1] For a summary see Johs. Schmidt (1932).

[2] Through this observation von Humboldt was led to conclude that a bank of benthonic *Sargassum* ("*Fucus* Bank") would have to be found to the west of the Azores and another to the South-West of Bermuda (see Winge 1923, p. 5), assumptions which have since been thoroughly refuted by the development of our knowledge of the geography of the Atlantic Ocean.

[3] Meyen, Thunberg, Harvey, Leps, Martens, Perrier, Schütt, Hentschel (see Winge 1923, pp. 6–7).

Spring	*Summer*	*Autumn*	*Winter*
159.5	148.9	189.6	177.2

It now becomes necessary to call to mind again the fact that these figures are only a cumulative expression of the frequency with which drifting weeds have been observed within each 1° coördinate unit, regardless of amount of weeds observed on each occasion. It is evident, of course, that the aggregation of the drifting weeds in relatively large rafts or floes with wide stretches of empty water between will serve to reduce the numerical frequency with which floating vegetation would be encountered, and will therefore serve to reduce the number of entries in records of the sort upon which Krümmel's and Antze's figures are based. It is also obvious that periods of relatively calm weather will favor the concentration of the drifting weeds into larger and larger aggregations, reducing the *frequency* of the rafts as their average size increases, and that the onset of greater surface disturbances in the fall will serve to break up and disperse the larger rafts even more than it affects the partitioning of the individual plants.[2] In the author's opinion, the continued decline in the frequency of pelagic *Sargassum* observations during the warm season until the sudden increase occurs in the fall is probably largely to be explained in this manner as an expression of the annual cycle in the number and average size of the weed-patches, and is only to a much lesser extent due to fluctuations in the number of individual plants, while it is not at all *directly* connected with seasonal variations in the total bulk of the floating vegetation.

It might also be mentioned at this point that such variations in degree of dispersal or aggregation of the floating weeds will, of course, have a geographical as well as a seasonal aspect and may perhaps serve to explain some of the irregularities in the geographical distribution of the Krümmel-Antze frequency values.

---

[1] The figures represent the sums of the Krümmel-Antze frequency percentages per 5° geographical coördinate unit, 45 such units being included in the entire Sargasso Sea area.

[2] The concentration of the weeds during calm weather into large, more or less circular rafts, offering the least statistical chance of intercept with the course of a ship, and their dispersal by the wind into thinner and thinner stripes and single plants or small tufts, has been fully described by Winge himself (1923, pp. 11–12) and his observations are entirely in accordance with our own.

4) The proponents of the theory of an enduring pelagic existence have with perfect justification pointed to the inability to find any benthonic fields of the pelagic weeds of an extent and abundance which would be at all adequate to account for the large amount of floating plants on the assumption that their pelagic existence was of a short duration and this we shall attempt to elaborate further in the following pages. One weakness in this line of reasoning has been the uncertainty as to the identity of the benthonic forms from which the pelagic weeds might be derived. As a result of the present investigation, this problem has now been solved for one of the two floating species which make up the bulk of the pelagic flora, but the discovery of its benthonic counterpart has merely served to strengthen the argument concerning the inadequacy of the benthonic flora to explain the pelagic one, since this benthonic form is certainly not a common variety even among the generally apparently rather scanty sessile *Sargassa.*

In regard to the arguments which have been raised against the theory of an essentially self-sustained pelagic *Sargassum* community it seems sufficient to say that these have all been so adequately refuted by Winge and others whose work he reviews and refers to, and in whose reasoning the author entirely concurs, that no valid specific objection based upon actual facts really remains to be disposed of today.[1] The criticism which still has to be met is mainly that of a purely negative skepticism, healthy in any field of research, springing in this case from an unwillingness to entertain the possibility of an indefinitely protracted pelagic existence of a sterile vegetation which evidently never resorts to reproductive processes of multiplication. And even this attitude of skepticism can scarcely be said to be entirely in accordance with all general knowledge since life apparently indefinitely sustained and multiplied by vegetative processes, only, is certainly not unknown in botany from many examples other than the Sargassa, even among higher plants.

That the eupelagic weeds always lack organs of fructification in their floating existence was first observed by Meyen (1884) and has been fully confirmed by every subsequent investigator, except Küntze (1881), whose claims to have found fertile pelagic specimens in his collections have already been discredited by Winge (1923, p. 20). To add our own experience to the cumulative evidence from the experience of others, we may say that among the thousands of eupelagic weeds sorted in the course of the investigations here reported upon we have not seen one single *unattached* fertile plant, and only in the one instance of a specimen of *S. fluitans* floating attached to a piece of mangrove root (?) in the marginal zone of the Sargasso Sea were organs of fructification found to be present (see p. 49).

---

[1] The tendency for refuted contentions to survive in the general literature is unfortunately fairly universal. Thus Küntze's unfortunate claim to have disproved the existence of any Sargasso Sea at all reappears as a statement disposing of the entire phenomenon in a work as recently published as J. E. Tilden's "The Algae and their life relations," University of Minnesota, 1935 (page 334).

It is interesting to note that Meyen, who first observed the sterility of the floating weeds, was nevertheless also the first writer to suggest that the pelagic plants may continue to live, grow, and multiply by partition indefinitely (for thousands of years), carrying the theory so far in fact as to assume that the quantity of weeds in the Sargasso Sea must be constantly increasing.

Perhaps a few simple mathematical considerations may serve to clarify the problem and make the conclusions arrived at more acceptable on the basis of general knowledge.

If we assume that there is a constant annual recruitment, a, torn off from the bottom to form the pelagic community, and that the floating vegetation suffers a constant annual loss, d, by mortality in excess of growth increment, d being expressed as a fraction of the vegetation present at the beginning of each year (fraction of 1), then the size of the total pelagic population, P, when it has reached equilibrium between annual recruitment and annual net loss will obviously be expressed by the equation:

$$(1) \qquad P = a + a\,(1 - d) + a\,(1 - d)^2 \ldots\ldots\ldots + a\,(1 - d)^n$$

in which $a\,(1 - d)^n$ expresses the reduced size of a given annual recruitment from the bottom after n years afloat. To get the average age in the pelagic state, D, of the entire drifting vegetation we must therefore weight (multiply) each term (remnant of an annual recruitment) on the right side of equation (1) by its age afloat and divide the expression thus obtained by the entire size of the pelagic population as given in (1), thus:

$$(2) \qquad D = \frac{0.a + 1.a\,(1 - d) + 2.a\,(1 - d)^2 \ldots\ldots\ldots + n.a\,(1 - d)^n}{a + a\,(1 - d) + a\,(1 - d)^2 \ldots\ldots\ldots\ldots\ldots + a\,(1 - d)^n}$$

Substituting $k = 1 - d$ and eliminating a we get

$$(2a) \qquad D = \frac{k + 2k^2 \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots + nk^n}{1 + k + k^2 \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots + k^n}$$

adding 1 and treating it as an infinite series we obtain

$$(2b) \qquad D + 1 = \frac{1 + 2k + 3k^2 \ldots\ldots\ldots\ldots\ldots\ldots\ldots}{1 + k + k^2 \ldots\ldots\ldots\ldots\ldots\ldots\ldots}$$

or, since the enumerator in (2b) is simply the second power of the denominator

$$(2c) \qquad D + 1 = 1 + k + k^2 \ldots\ldots\ldots\ldots\ldots\ldots\ldots$$

and, since the expression on the right side of equation (2c) for an infinite series approaches the limiting value of $\frac{1}{1-k}$ *, this gives:

$$D + 1 = \frac{1}{1-k} \qquad \text{or} \qquad D = \frac{1}{1-k} - 1$$

Introducing again $d = 1 - k$ we thus have

$$D = \frac{1}{d} - 1 \tag{3}$$

If we now go back to equation (1), substitute $k = 1 - d$, and introduce the limiting value $\frac{1}{k-1}$ for the series $1 + k + k^2 \ldots\ldots\ldots\ldots + k^n$ we obtain

$$P = a\left(\frac{1}{1-k}\right)$$

Substituting again $d = 1 - k$ and solving for d this gives

$$d = \frac{a}{P}$$

Substituting for d in (3) we have

$$D = \frac{P}{a} - 1 \tag{4}$$

From this equation it is evident that if the average duration of the pelagic phase should be one year only, the annual recruitment must equal one half of the entire floating vegetation. A six months average duration would require an annual recruitment equal to two-thirds of the total vegetation. Conversely an annual recruitment of one-tenth of the floating vegetation corresponds to an average lifetime afloat of 9 years.

Having tentatively established in the preceding chapter that the total pelagic *Sargassum* vegetation is apparently on the order of magnitude of 5–10 million metric tons, wet weight, we may now proceed to discuss whether it is at all conceivable that the annual recruitment could be in a proportion to this total amount which would indicate a short average duration of the pelagic phase according to equation (4).

(A) Considering first the possible sources of benthonic weeds, we immediately find these to be very restricted both in extent and in richness of flora from which the pelagic forms may be derived. The coastal areas in the Eastern Atlantic, limited under any circumstances to the outlying islands of the Azores, Madeira and the Canaries have already been eliminated from discussion in the previous literature due not only to their insignificant extent but also to the fact that they do not actually fall within the Sargasso Sea proper, but are barely touched by its extreme boundary in the case of the Azores and fall entirely outside of the region of the floating weeds in the case of the other islands. We can therefore confine ourselves to the question of possible benthonic sources in the Western Atlantic.

---

* K being only a fraction of 1.

The fact that the Caribbean area south of Jamaica and Honduras is empty of floating weeds excludes the coasts of the Lesser Antilles and the South American continent from quantitative consideration. There remains then in the East only the coasts of the Greater Antilles, the Bahamas, Florida, the Gulf of Mexico and Bermuda, and the banks between Jamaica and Honduras.

(B) Within these coastal belts algae of the type of *Sargassum* can, of course, only occupy a relatively shallow belt. The literature does not seem to contain any unquestionable records of sessile *Sargassum* from depths over 50 meters and it does, at all events, on the basis of present knowledge, seem extremely unlikely that there can be any quantitatively significant *Sargassum* flora below this depth, but for the sake of the argument we may consider the entire zone down to 100 meters depth as being potentially inhabitable by benthonic *Sargassa.* From the available hydrographic charts the total area of this zone along the coasts and on the banks mentioned above has been estimated as somewhat less than 220,000 square miles. Inclusion of all areas down to 200 meters depth would not change this amount in any significant manner, due to the prevailing shape of the bottom contours, nor would exclusion of all areas below 50 meters depth change its order of magnitude, although it would result in a more appreciable reduction in the amount. Taking all factors and allowances into consideration, the author is inclined to believe that the estimate above given cannot be much less than twice the actual potential area of vegetation. It might furthermore be pointed out that quite probably several large areas here included, such as the northern bank in the Gulf of Mexico should actually have been excluded from consideration in relation to the pelagic flora for hydrographic or other reasons. However, we may let the estimate stand as a maximum figure of potential vegetation area, with reference to depth, in the order of magnitude of hundreds of thousands of square miles, or more precisely about 200,000 square miles.

(C) But this large area is far from being uniformly covered with a blanket of *Sargassum* vegetation. Quite to the contrary, the local fields of sessile *Sargassa* have to be patiently and diligently searched for in most regions. In the first place at least half of the total area included in the figure arrived at under point (B) consists of *large continuous stretches* of fine sands and muds entirely unsuitable as a substratum for sessile *Sargassum,* and in the stretches defined as "shell and sand" or "coral and sand," which constitute by far the greater portion of

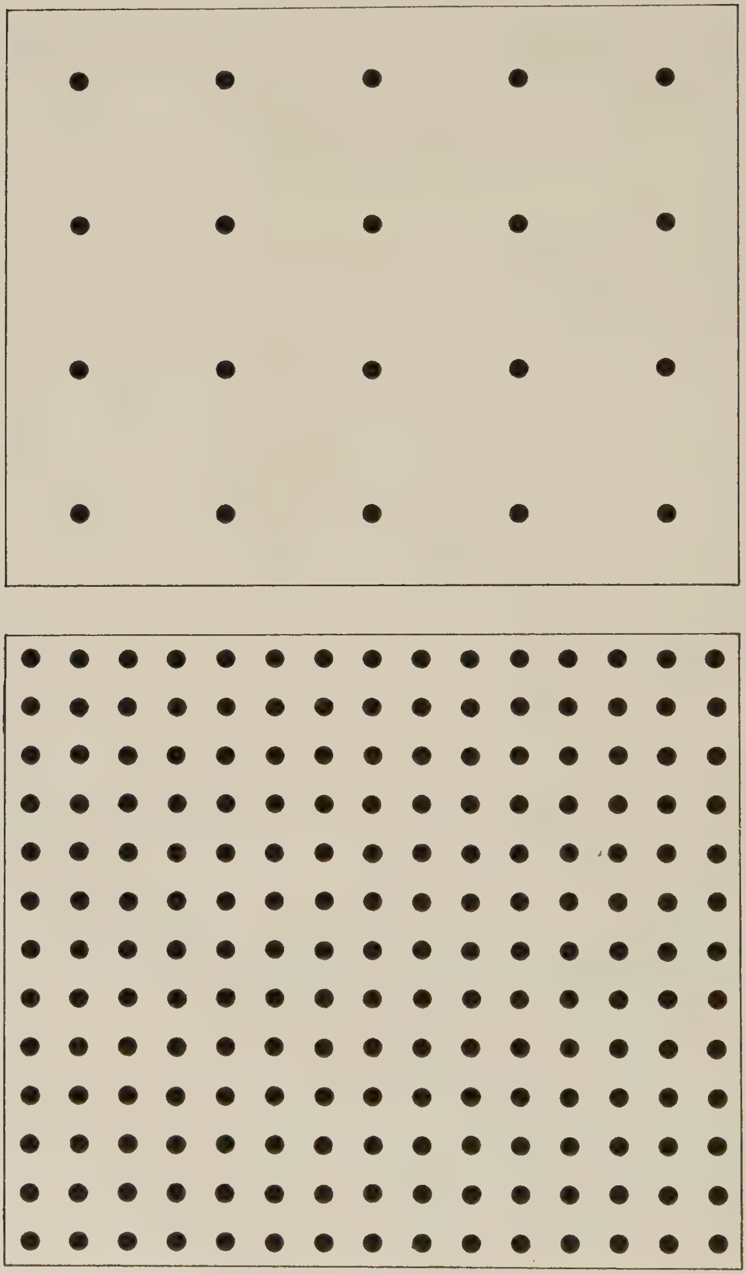


Figure 33. Left square: black dots covering about 1/10 of area. Right square: black dots covering about 1/100 of area.

the other half, fine sand undoubtedly covers by far the largest part of the actual area. The 200,000 square miles above the 100 meter contour line can thus, extremely conservatively, be reduced to about 50,000 square nautical miles potentially inhabitable by benthonic *Sargassa.* If, further, the author's experience in shallow-water collecting in the regions here considered is any index of the frequency of the weeds, even those portions of the total area from shore to 100 meters which may be considered in a general way, i. e., spotwise, inhabitable by *Sargassum* are actually covered only to an extent to be reckoned in hundredths of their total area. Since quantitative data are not available, and are probably impossible to obtain at any time in view of the character of the bottoms with which we are here dealing, a simple visual presentation of 1/10 and 1/100 as coverage given in figure 33 may perhaps help the reader in evaluating his own impressions. If the coverage should be on the order of magnitude of tenths of the area, the reader's impression of the average density of *Sargassum* inhabitation on suitable bottom throughout the Central American region must correspond at least to the density shown in the right part of our diagram, or to a multiple of this density. If the reader's impression is of a density intermediate between those shown in the left and in the right part of our figure, then a coverage to be reckoned in hundredths of the area is implied. For the purpose of our discussion, we shall merely assume that the average density throughout the inhabitable half of the bottoms of the coastal belts here considered does not exceed *twice* that shown at the right of our figure, or one-fifth coverage, which, in the writer's opinion is probably nearly 10 times the actual coverage. By this generous allowance for coverage, which the author is convinced will be more than acceptable to anybody experienced in shallow-water collecting in these waters, combined with our reduction of potentially inhabitable area to 50,000 square miles, or less, the order of magnitude of the possible area actually covered by benthonic *Sargassum* vegetation has now become reduced from hundreds of thousands to tens of thousands of square miles, more precisely to about 10,000 square miles, or less. And it seems most probable that we have at this point left a margin of safety for our further calculations on the order of the ratio of 10 : 1.

(D) But as already pointed out by others, and abundantly confirmed by the collections of benthonic *Sargassa* available to the writer, the benthonic forms from which the pelagic weeds *may* be derived are not those which occur most abundantly where a sessile flora is found. On the contrary, so far as present knowledge indicates, the benthonic form from which we now know that the pelagic *S. fluitans* (see page 49) may be recruited must certainly be very limited in its occurrence in the sessile fields so far investigated, and we have no definite knowledge as yet of any form at all being taken on bottom which may with any assurance be considered the "parental" form of the pelagic *S. natans.* The species (or varieties) constituting the overwhelming majority of all available records and collections of the benthonic flora so far as known today are particularly *S. filipendula*, *S. polyceratium*, *S. pteropleuron*, *S. hystrix* and to a lesser extent those forms of *S. vulgare*, which can be definitely ruled out as contemporary sources of the pelagic weeds. On the basis of today's knowledge, at least, we may thus safely assume that weeds from which the pelagic forms may possibly be recruited comprise less than one-tenth of the entire benthonic flora; in other words they occupy less than 1/10 of the area of vegetation already limited by previous reasoning to less than 10,000 square miles, i. e., the possible source of floating weeds must cover an area of an order of magnitude of only one thousand square miles, *or less*.

(E) But if an area of benthonic vegetation[1] reckoned only in thousands of square miles should make an annual contribution to the pelagic flora reckoned in millions of tons, as required if the average duration of the pelagic phase is only to be reckoned in years (not tens of years) (see (4) page 74) it would have to surrender an annual yield on the same order of magnitude as the total average crop of a terrestrial vegetation, or the total annual phytoplankton production in the upper 70 meters in such a productive region as the British Channel,[2] that is a yield on the order of magnitude of thousands of tons per square mile. It seems very unlikely, of course, that the total production of a sessile algal flora can ever remotely approach the production of total phytoplankton, or a total terrestrial vegetation, but for the sake of the argument we may at this point assume that it might possibly at least be on the same order of magnitude.

(F) But allowing for the possibility of this extremely improbable, high order of productivity of the benthonic vegetation, we would also have to assume a 100 per cent effective harvesting of this production by storms and wave action to make the yield available to the pelagic flora, and also that this harvesting was the only significant source of loss to the benthonic vegetation. Both assumptions would be patently absurd. Although the violent hurricanes of the West Indian region may unquestionably be very effective in tearing loose sessile vegetation, they undoubtedly are not on the average 100 per cent effective even in their direct path, although they might achieve this efficiency in certain places. If they were, the maintenance of the benthonic flora would become a problem even more disturbing than that of the pelagic vegetation. The paths of the hurricanes in an average year will, moreover, only cover a fraction of the entire coastal area with which we are here concerned. Storms of lesser intensity cover wider areas, of course, but also with less efficiency. A very considerable amount of the weeds torn loose from the bottom will further be removed from our consideration by being immediately thrown ashore to destruction. At this point one should bear in mind that the most effective wave-action, or one might perhaps even say the only effective wave-action in the shallow-water belt, will be obtained from a wind direction with an on-shore component, which, *ipso facto*, should be expected to deposit the better part of its harvest directly upon the adjacent shores. Taking all things into consideration, it certainly seems very improbable that wave-action should be able to *harvest and successfully bring into* the pelagic population more than at most 1/10 of the total annual production of the benthonic vegetation. But now we are down to an annual contribution from benthonic fields to the pelagic phase on an order of magnitude of tenths of the total pelagic population, even assuming a *benthonic* productivity at least on the same order of magnitude as the productivity of terrestrial vegetation or the total productivity in the British Channel.

---

[1] Of forms which might form the source of the pelagic weeds.

[2] The estimates given by Atkins (1923) indicate a production of somewhat less than 5000 tons per square nautical mile.

In other words, it would be beyond all reason to assume that there are sources of benthonic vegetation adjacent to the Sargasso Sea which could make an annual contribution to the pelagic population on an order of magnitude greater than one-tenth of the order of magnitude of the pelagic population itself; and that therefore in accordance with equation (4) (page 74) it seems inconceivable that the average duration of the pelagic existence should have to be reckoned in less than tens of years (at least 10), probably in hundreds or thousands.

There is also another approach to the determination of at least the order of magnitude of the average duration of the pelagic existence through an approximate evaluation of the size of the annual contribution a to the pelagic flora from direct observational records. It is obvious, of course, that weeds torn loose from the bottom will retain, in a recognizable form, various features of general habitus, characteristic of their sessile phase, for a certain length of time after they have entered their pelagic existence. These features are particularly associated with polarity of growth, which in the sessile form is a polarity of the entire plant with reference to a single plane, the horizontal, or the solid substratum, but in the pelagic weeds of long standing is merely a ploarity of parts (branches, etc.) with reference to an axis, or a system of axes, represented by stems and branches. There are also other characters more difficult of definition but easily recognized on actual specimens. Since the change from benthonic to pelagic habitus can only be accomplished through growth, it probably requires a very considerable period of time (see Winge 1923, p. 20). Certainly those who are willing to doubt the ability of the floating weeds to form a self-sustaining population by vegetative growth must also be more than willing to grant this point. If we assume then that the floating weeds will retain recognizable evidence of their recent derivation from the bottom for 1/10 of a year, the weeds in our pelagic collections thus recognized should represent approximately 1/10 of the annual contribution from the benthonic vegetation to the pelagic flora. But in the case of the *S. natans* series of floating weeds, the total amount of plants observed with any indication of an at all recent derivation from the bottom is less than one-thousandths (1/1000) of the total amount collected, when we allow for the possibility that this entire series might be derived via the form of *S. natans VIII*, described on page 46. If *S. natans I*, constituting more than 9/10 of the pelagic volume of this series should not be derived in this manner, the indicated contribution from bottom for 1/10 of a year is even less than 1/1000, in fact it is absolute 0. For the *S. natans* series the value of the annual recruitment a in our equation (4) (page 74) thus seem to be less than 10/1000 or 1/100 of the floating population P, and the average duration of the pelagic existence for these weeds D should consequently be at least one hundred years, or more.

In the case of the *S. fluitans* series, the problem becomes somewhat complicated by the question of the extent to which the form *S. fluitans X* as a whole should be considered as showing evidence of recent derivation from a benthonic existence. By far the greater portion of *S. fluitans X*, however, has already lost its benthonic and developed a pelagic polarity, and if we include, with generous allowance, only those plants of *S. fluitans X* and *III* which definitely show the kind of evidence of recent benthonic derivation mentioned above, we are also in this case down to an order of magnitude for the 1/10 annual contribution of thousandths, only, of the total pelagic stock,[1] *i. e.* to an amount to be reckoned only in fractions of hundredths, putting the entire annual contribution a at fractions of 1/10 of the population P, and the average duration D of the pelagic life of *S. fluitans* at least at multiples of 10 years, approaching 100 years or more.

From an entirely different set of premises we thus again arrive at the conclusion that the average duration of the pelagic existence must probably be at least multiples of 10 years for *S. fluitans*, and 100 or a multiple of 100 years for *S. natans*, and it does not seem as though any reasonable allowance for seasonal variations (our data being mostly gathered during the early spring) or other possible errors in our second method of approach could bring this minimum value down to less than 10 years for either group of eupelagic weeds, certainly not under any circumstance in the case of *S. natans*.

In the preceding discussion we have dealt with the possible total cumulative loss by mortality[2] in excess of increment by vegetative growth, d, suffered by the entire pelagic population over its entire area of distribution, having for convenience assumed this loss to affect equally all pelagic year-classes, *i. e.*, all annual contingents from the benthonic vegetation regardless of the past duration of their pelagic existence. It now becomes necessary to look into the nature of this loss by mortality and in particular to inquire into the extent to which it may prove to be geographically limited or at least a geographical variable. The author's conclusions on this point may be very briefly stated. In all the collecting on which this report is based no evidence suggestive of any mortality of entire plants was noted among the eupelagic weeds in their oceanic domain, south and east of the so-called "Gulf Stream," *at sea* between Bermuda and the Antilles. That is, we have never, in the Sargasso Sea proper, seen any evident degeneration of the plants themselves, such as that observed in other waters, nor any over-incrustation which might threaten to submerge an entire weed. The observations recorded on page 10, showing how strictly their buoyancy confines the floating eupelagic *Sargassa* to the very surface alone, might also be referred to at this point since they also, within their limitations, serve to show the absence of plants approaching equilibrium with the specific gravity of sea water as an initial step towards their destruction by sinking. In other words, the assumption of a heavy mortality in the Sargasso Sea proper seems purely speculative and quite discordant with any observable evidence. That some loss will occur in the form of the sinking of basal fragments of a plant which may become severed from their connections with the buoyant distal portions, when the weed "multiplies" by a mechanical breakup is evident, but there is no reason whatsoever to assume that this loss is not adequately compensated for by the growth of the younger distal parts which remain afloat. The more so since we can only assume that it is mainly through the increased size of the entire plant due to this distal growth that the stress on its stems in the action of the waves reaches the point where fragmentation is likely to occur. In the author's opinion it is essentially only through the chance of their drifting away from the central area into the marginal zone, and even onto the shores, that death of the entire plants threatens the weeds which have once arrived in the Sargasso Sea proper.

---

[1] But not to *less* than 1/1000 as in the case of *S. natans*.

[2] Sinking due to loss of buoyancy or excess weight of epizoan fauna is, of course, included as a form of death in our use of the term mortality throughout these pages.

The marginal zones of mortality during mid-winter and the very early spring apparently include at least the northern half of the Gulf of Mexico, the entire Gulf Stream north of Florida, in particular the expanse between Bermuda and Cape Cod, and the northern boundary of the Sargasso Sea in general; and in these waters obvious degeneration of the entire plants can be abundantly observed also among the eupelagic weeds still floating on the high seas. The plants commonly appear dark brown and battered, seem to suffer considerable losses of leaves and bladders, and give little or no indication of fresh distal growth.[1] It seems most probable, of course, that low temperatures must be the main causative factor of this degeneration. Winge (1923, p. 18) makes the statement that [pelagic] *Sargassum* apparently cannot thrive in a temperature lower than 18° C., but in the author's opinion it is insufficient to look for an explanation of their distribution in the seawater temperatures alone, for the reason that the weeds through their buoyancy are actually always in part above the surface of the water directly exposed to the air, although only by a very small fraction of their mass at a time. In this manner portions of a plant may have been exposed to a chilling from the cold winter storms frequent in the Gulf of Mexico and in the other marginal zones above mentioned, of which we would find no adequate indication in the surface temperatures of the sea. The parts which would first be exposed to these detrimental effects would naturally be the most buoyant, which are normally the most distal ones in which the potentiality of future growth is also located. If the parts thus exposed are killed and disintegrate or fall off, other buoyant parts would then turn towards the suface to be similarly destroyed, the basal or central parts of the weed, with the least buoyancy, always remaining the longest, until the buoyancy of the entire plant has become reduced to the point where the final remnant ultimately sinks to its destruction. Probably this process of gradual, rotating killing of distal parts by exposure to air temperatures and chilling winds is the explanation of the ball-like degenerating weeds consisting chiefly or entirely of proximal parts only, with relatively few leaves and bladders left, which we have often observed in the Gulf of Mexico.

---

[1] This description, of course, applies only to the plants which are presumably dying. The marginal zones above mentioned are by no means entirely free from healthy-appearing weeds even in mid-winter.

Weeds which have been washed ashore and washed off again before their decay had been completed, and which therefore continue their degeneration at sea will, of course, also have to be reckoned with in the marginal zones.

During summer the Gulf of Mexico can probably be eliminated as a region of temperature-death in open sea, and the lethal zone will be shifted farther to the West of the Gulf Stream boundary and to the North and East of Bermuda, but the fact remains that the western boundary of this current and the area towards which its main flow is directed will all year round represent the main regions of mortality for the pelagic flora, since these are the regions in which the floating weeds will be most rapidly, and in greatest bulk, brought into contact with unfavorable temperature conditions. That a very considerable amount of weeds is actually carried into these lethal regions is amply shown by our own collecting in the cross-section between Cape Cod and Bermuda, both in the summer (healthy weeds at this point) and in the winter (many unhealthy specimens among healthier ones) and the further transportation to the North-West into still more dangerous waters is clearly indicated by the tongue-like extension of the boundaries of pelagic *Sargassum* occurrence to the NW of Bermuda, shown in Winge's map (Winge, 1923, fig. 2).

It is evident that the weeds most likely to be carried by the Gulf Stream into these areas of dangerous temperatures are those which have just started their pelagic existence within the very waters of current system with which we are dealing, that is, the fresh annual contingent from the benthonic flora of the Antillean, Central American and Southern North American coasts; while the likelihood of the plants which have already safely reached the central regions of the Sargasso Sea being returned to its Gulf Stream boundary is, of course, considerably less, although still significant. The recently detached benthonic recruits to the pelagic flora which have escaped the danger of being immediately washed ashore, therefore still have to survive the hazards of the northward flow in which they find themselves, and through which they undoubtedly must suffer a considerable reduction in numbers, before they can actually be said to have become definitely a part of the pelagic population. For observational confirmation of this speculative deduction, we may refer to the fact that the occurrence of all the rapidly perishing holobenthonic weeds, and also of the relatively long-lived quasi-pelagic *S. hystrix* is strictly confined to the region of the Gulf Stream system (Winge 1923, as well as our own observations), thus showing no evidence of a significant direct translation across the current into the central region of the Sargasso Sea proper. We may further point out that all the specimens of eupelagic weeds showing any possible indication whatsoever of a fairly recent derivation from bottom have also been found exclusively in the region of the Gulf Stream system.[1] It therefore seems possible to state with a fair amount of assurance that a large part if not the bulk of the presumptive annual contribution from benthonic vegetation to pelagic flora will be forced to traverse the dangerous region North and East of Bermuda before actually becoming incorporated in the population of the Sargasso Sea proper. It is therefore probable that only a very much reduced contingent finally achieves this goal, or in other words that the loss by mortality in excess of vegetative growth is not equally distributed on all pelagic year classes but affects chiefly the new contingent or O-class, and that the average expectancy of duration of the pelagic existence for the older contingents which have once successfully escaped the hazards of the Gulf Stream drift and arrived in the Sargasso Sea proper is therefore very much *i. e.*, probably many times, greater than indicated in our estimates of minimum possible average duration for the entire pelagic population including the O-class still floating in the marginal zone.

For the assumption that a relatively heavy mortality does occur in the region North and East of Bermuda, particularly North of 40° latitude, we have our own observations of an increasing frequency of unhealthy-looking weeds north of Bermuda during winter, and we may also refer to Krümmel's observation (Krümmel, 1891, p. 138) that pelagic weeds are found north of 45° latitude only in late summer and fall, but not during the rest of the year. Krümmel interpreted this as evidence of a periodic (seasonal) contribution from the benthonic vegetation farther south which in the normal course of events would reach these higher latitudes at that time, but Winge (1923, pp. 15–16) has shown the lack of necessity for resorting to this assumption in explanation of this particular phenomenon, and has in general proved the incorrectness of Krümmel's theory.

---

[1] We here include in this term the entire territory of the Central American Seas, including also the outer coastal waters of the Bahamas and Antilles, swept by the Antilles Current which joins with the Florida Current before Cape Hatteras to form the so-called "Gulf Stream."

Winge instead refers the disappearance of the pelagic weeds from the higher latitudes during late fall and winter to the onset of the North and Northwesterly winds of the cold season. While it is quite possible that these winds might drive some surviving weeds back to lower latitudes, it is also evident that they would at the same time provide a most effective chilling mechanism for the destruction of the weeds under their influence. With some allowance for the factor of regressive transportation in terms of latitude the author therefore sees in Krümmel's observations mainly the effect of a shifting southward of the lethal zone during the cold season. Finally, one may *a priori* submit that if a relatively high degree of mortality is not to be found at the northern cold boundary of the Sargasso Sea towards which a major portion of the new contingents from the benthonic fields are driven, it would be preposterous to assume the existence of any significant mortality contrary to all appearances in the central area of the Sargasso Sea proper. Arguments against the assumptions on this particular point would therefore be arguments in favor of the main conclusion in regard to the longevity of the sterile floating weeds, in which the author joins such previous investigators as Krümmel and Winge themselves, Meyen, Hentschel and others.

While it thus seems evident that the annual contingent actually received in the Sargasso Sea proper is certainly very small in proportion to its entire pelagic *Sargassum* population, it is on the other hand also obvious that such a contribution from benthonic vegetation, however small, if it actually does exist[1] must serve to increase the total floating population until a balance is reached where it compensates for the loss by mortality in excess of the vegetative increment and multiplication of the entire pelagic stock. And it would be unreasonable to assume that the pelagic population has not been in existence for a sufficiently long time to have reached this equilibrium between loss and recruitment today.

Through the reasoning explained in the preceeding we therefore arrive at the conclusion that the pelagic *Sargassum* population of the so-called Sargasso Sea, apart from its marginal zones, is probably an essentially self-sustaining unit with a potentially infinite longevity and a very long normal expectancy of life for its individual plants, receiving (*at most*) only a very slight annual contribution from benthonic vegetation merely sufficient to compensate for its own loss by a slight excess of mortality over vegetative growth increment, suffered mainly through a continually occurring chance return of some of its members to the dangerous marginal zones from which a corresponding recruitment of freshly detached plants which have escaped its hazards are received in exchange.

[1] The author is as yet inclined to consider it in terms of a possibility only, at least insofar as *Sargassum natans* is concerned.

LIST OF HAULS MADE WITH PELAGIC WEED COLLECTOR

The following list is a definitive account with regard to the amounts of the dominant forms of pelagic weeds obtained in the individual hauls. That is to say, it presents the final figures and notes concerning the presence and abundance, or the absence, of *S. natans* (*I*) and *S. fluitans* (*III*), or of *S. fluitans* as a whole (*III* + *X*) where no distinction has been made between the two forms in which this species may occur. The list is also final with regard to the abundance of any other type of *pelagic Sargassum*, wherever such other forms were obtained in sufficient quantity to be recorded by weight. In addition to these definitive *quantitative* figures one will also find entries of all notes so far made, whether on shipboard or during the subsequent examination of the preserved material, concerning the mere presence of the rarer forms in amounts too small to be weighed. These non-quantitative records of the mere presence of a form cannot, however, be guaranteed to be entirely complete, in view of the vast amounts of weeds which had to be sorted on board, and thereafter discarded, and of the likewise very large amount preserved. It is quite likely that the reexamination of the preserved material alone, planned in connection with the final systematic analysis after sufficient benthonic collections have also been obtained, will increase the number of records of rarer weeds present in individual hauls.

There is also considerable variation in the details given in the field-records of each haul. When made under instructions in the absence of the writer[1] the standard entries are simply the weights of "fine-leafed" (*I*) and of "coarse-leafed" (*III*) weeds, which, together with a total preservation of all unusual-looking weeds, and a random sample of the dominant ones, provides ample information for the purposes of this investigation.

When a small catch was preserved in its entirety, the weight of the separate forms was subsequently determined, after sorting in the laboratory, as the wet weight in formalin, which will not differ significantly from the wet weight of the fresh material. The weight of such small samples determined in the laboratory could naturally be recorded in more accurate figures than those used in the weighing of large samples on board (usually nearest ¼ pound). In other instances, when difficulties in sorting arose on board in the absence of the writer, the total weight of the descriptive category "coarse-leafed" or "large-leafed," was taken on board and entered in the field-record, with a specially large random sample preserved, from which the relative amounts of the forms combined in this category were subsequently determined in the laboratory. In the case of the hauls made in the Gulf of Mexico during 1935 (Nos. 172–188), *S. natans VIII* and *S. fluitans* were commonly combined in the field-records under the heading of "broad-leaved" weeds, and the weight recorded under this heading has only subsequently been divided according to the relative abundance of the two forms in the large random samples. In the Gulf of Mexico the true *S. fluitans* generally occurred only in such fragmentary (although not quantitatively insignificant) material that it was not found practical to attempt to distinguish between its two forms. The discovery of the actual identity between *S. fluitans III* and *X* (on 1934 winter-cruise material) also lessened the emphasis upon a separate sorting of these two forms. In the 1935 records *X* has therefore only been entered as a notation of its presence in the quantitative record of *S. fluitans* given under *III* (the always predominant form) when some well-developed plants of the *X* form were conspicuous in the catch.

---

[1] Hauls Nos. 1–113 and 141–172 were all made and sorted under the supervision of the writer with the assistance of the ship's company.

The following example may serve as an interpretation of the entries used in the records of the individual hauls.

Example:

#51. 1/27. 23°23.5′ N. 69°57.5′ W. 19.0 Mi. 44.00 I. 5.00 III. II. V. X.

Read:

Haul No. 51. January 27. Median latitude 23°23.5′ N. Median longitude 69°57.5′ W. Length of haul through the water (log-distance) 19.0 nautical miles.[1] 44.00 pounds of *S. natans* (*I*) (wet weight). 5.00 pounds of *S. fluitans* (*III*). *Sargassum II*, *V*, and *X* present in small amounts.

1933

SOUTH OF BERMUDA.

#1.	2/13.	31°25.5′ N.	66°45′. W.	3.0 Mi.	.50 I.	2.00 III.		
#2.	2/13.	31°24′ N.	66°52.5′ W.	8.0 Mi.	2.75 I.	9.75 III.		
#3.	2/13.	31°22′. N.	67° 3′. W.	10.0 Mi.	3.75 I.	13.50 III.		

SARGASSO SEA. NASSAU TO ANEGADA PASSAGE.

#4.	2/26.	25°38′ N.	75°16′ W.	14.1 Mi.	4.00 I.	6.50 III.	II.	X.
#5.	2/26.	25°36′ N.	75° 0′ W.	15.9 Mi.	12.00 I.	16.50 III.	2.00 X.	II.
#6.	2/26.	25°34′ N.	74°41.5′ W.	16.5 Mi.	12.25 I.	12.75 III.	1.25 X.	
#7.	2/26.	25°36.5′ N.	74°23′ W.	14.3 Mi.	8.50 I.	15.00 III.		
#8.	2/27.	25°46′ N.	72°35′ W.	14.4 Mi.	5.25 I.	15.50 III.	1.25 X.	II.
#9.	2/27.	25°46′ N.	72°23′ W.	8.0 Mi.	19.25 I.	56.00 III.	2.00 X.	
#10.	2/27.	25°45.5′ N.	72°15′ W.	6.7 Mi.	7.00 I.	4.00 III.		
#11.	2/27.	25°44.5′ N.	71°57′ W.	13.0 Mi.	.25 I.	8.00 III.		
#12.	2/28.	25°31.5′ N.	69°23′ W.	15.2 Mi.	21.00 I.	17.50 III.	2.50 X.	
#13.	2/28.	25°30′ N.	69° 5′ W.	17.0 Mi.	28.50 I.	22.00 III.	1.75 X.	.25 II
#14.	2/28.	25°29′ N.	68°49′ W.	13.0 Mi.	36.00 I.	28.50 III.	3.50 X.	
#15.	3/1 .	25°17.5′ N.	66°41.5′ W.	14.1 Mi.	19.75 I.	30.25 III.	.50 X.	
#16.	3/1.	25°17′ N.	66°23′ W.	17.2 Mi.	9.50 I.	10.50 III.	.50 X.	
#17.	3/1.	25°16′ N.	66° 7.5′ W.	7.1 Mi.	17.75 I.	35.00 III.	1.00 X.	
#18.	3/3.	23°19′ N.	62°30′ W.	16.7 Mi.	24.50 I.	20.25 III.	.25 X.	
#19.	3/3.	23° 5′ N.	62°40′ W.	9.4 Mi.	17.00 I.	20.50 III.	VIII.	
#20.	3/4.	22° 2.5′ N.	62°43′ W.	12.7 Mi.	4.50 I.	10.50 III.		
#21.	3/4.	21°51′ N.	62°46′ W.	9.2 Mi.	Less than 1 lb. total haul			
#22.	3/4.	21°42.5′ N.	62°44′ W.	6.7 Mi.	3.50 I.	30.00 III.		
#23.	3/5.	21° 8′ N.	62°13′ W.	18.0 Mi.	16.50 I.	16.25 III.		
#24.	3/5.	20°56′ N.	62° 8′ W.	10.7 Mi.	13.75 I.	16.75 III.		

---

[1] Not necessarily identical with the geographical length of the haul in the presence of significant currents.

1933

CARIBBEAN.

#25. 3/13.	16° 1′ N.	64°28.5′ W.	14.0 Mi.	No weed				
#26. 3/27.	17°25′ N.	71°40′ W.	21.4 Mi.	1.00 I.	1.00 III.			
#27. 3/27.	17°30′ N.	72° 6′ W.	31.5 Mi.	1.00 I.	1.00 III.			

CAYMAN SEA NEAR WINDWARD PASSAGE.

#28. 4/18.	20° 0′ N.	74°19′ W.	11.0 Mi.	.50 I.	.50 III.			
#29. 4/18.	19°51′ N.	74°36′ W.	27.8 Mi.	2.00 I.	.50 III.			

1934

CAPE COD TO BERMUDA.

#30. 1/22.	36°21′ N.	66°39′ W.	5.9 Mi.	.70 I.	2.40 III.	V.		
#31. 1/22.	36°18′ N.	66°21′ W.	36.8 Mi.	.50 I.	11.00 III.			

SARGASSO SEA. BERMUDA TO TURKS ISLAND.

#32. 1/23.	31°57′ N.	65°52′ W.	14.5 Mi.	21.50 I.	12.50 III.	X.		
#33. 1/23.	31°44′ N.	66° 2′ W.	14.0 Mi.	6.50 I.	5.25 III.			
#34. 1/24.	30° 9′ N.	66°51′ W.	8.0 Mi.	18.50 I.	1.00 III.			
#35. 1/24.	29°96′ N.	66°53′ W.	19.7 Mi.	30.00 I.	5.00 III.	II.		
#36. 1/24.	29°38′ N.	67° 0′ W.	14.8 Mi.	46.50 I.	10.00 III.	II.		
#37. 1/24.	29°26′ N.	67° 9′ W.	16.8 Mi.	33.25 I.	3.00 III.	1.00 II.		
#38. 1/24.	29°11′ N.	67°17′ W.	15.2 Mi.	51.00 I.	5.00 III.	II.		X.
#39. 1/25.	27°46′ N.	68° 6′ W.	19.4 Mi.	49.00 I.	4.25 III.	.50 II.		X.
#40. 1/25.	27°33′ N.	68°10′ W.	5.8 Mi.	103.00 I.	3.00 III.	2.50 II.		X.
#41. 1/25.	27°28.5′ N.	68°13′ W.	5.7 Mi.	71.00 I.	6.25 III.	1.00 II.		X.
#42. 1/25.	27°21.5′ N.	68°16′ W.	7.5 Mi.	123.00 I.	6.75 III.	2.25 II.		VIII.
#43. 1/25.	27°18′ N.	68°18′ W.	2.6 Mi.	118.00 I.	6.25 III.	2.50 II.		V.
#44. 1/25.	27°13′ N.	68°20′ W.	7.7 Mi.	16.00 I.	1.75 III.	II.	V.	X.
#45. 1/25.	27° 5.5′ N.	68°23′ W.	5.8 Mi.	1.25 I.	.75 III.			
#46. 1/26.	25°50.5′ N.	68°56′ W.	18.0 Mi.	127.00 I.	9.50 III.	.60 II. V.		.80 X. VIII.
#47. 1/26.	25°33′ N.	68° 2′ W.	19.7 Mi.	100.00 I.	4.25 III.	1.50 II.		.90 X. VIII.
#48. 1/26.	25°12.5′ N.	69°12′ W.	20.0 Mi.	46.00 I.	5.00 III.	1.10 II.		V. X
#49. 1/26.	24°56.5′ N.	69°19′ W.	13.0 Mi.	79.00 I.	6.00 III.	.90 II.		.60 X.
#50. 1/27.	23°48′ N.	69°46′ W.	30.5 Mi.	33.00 I.	8.75 III.	II.	V.	X.
#51. 1/27.	23°23.5′ N.	69°57.5′ W.	19.0 Mi.	44.00 I.	5.00 III.	II.	V.	X.
#52. 1/27.	23° 5′ N.	70° 8′ W.	24.3 Mi.	89.00 I.	10.00 III.	II.	V.	X.
#53. 1/27.	22°46′ N.	70°20′ W.	18.2 Mi.	128.00 I.	14.00 III.	II.	V.	X.
#54. 1/27.	22°28′ N.	70°32′ W.	23.5 Mi.	50.00 I.	3.00 III.	II.	V.	X.
#55. 1/27–28.	21°58′ N.	70°52′ W.	46.0 Mi.	94.00 I.	4.00 III.	II.	V.	X.

TURKS ISLAND TO WINDWARD PASSAGE.

#56. 1/28.	21°37′ N.	71° 9′ W.	7.0 Mi.	3.00 I.	.80 III.			
#57. 1/28.	21°27′ N.	71°15′ W.	14.6 Mi.	16.00 I.	1.10 III.			
#58. 1/28.	21°13′ N.	71°21′ W.	18.4 Mi.	72.00 I.	2.25 III.	II-VIII.		X.
#59. 1/28.	20°56′ N.	71°38′ W.	32.4 Mi.	120.00 I.	7.00 III.	II.		
#60. 1/28.	20°42′ N.	72° 4′ W.	19.1 Mi.	1.00 I.	1.50 III.	VIII.		

CARIBBEAN I. WINDWARD PASSAGE TO PANAMA.

#61. 1/29.	19°53′ N.	73°27′ W.	43.3 Mi.	12.00 I.	4.00 III.	II.	V.	
#62. 1/29.	19°24′ N.	74°10′ W.	69.2 Mi.	3.00 I.	.80 III.	VIII.		
#63. 1/29.	18°57.5′ N.	74°44′ W.	17.6 Mi.	1.00 I.	.20 III.	II.		
#64. 1/29–30.	18°26.5′ N.	75°23′ W.	76.0 Mi.	10.00 I.	2.00 III.			
#65. 1/30.	17°52′ N.	76°16′ W.	46.3 Mi.	3.50 I.	Few sprigs III.			
#66. 2/2.	17°35′ N.	76°39′ W.	17.4 Mi.	2.40 I.	.30 III.	.20 II.		X.
#67. 2/2(–3).	17°20′ N.	76°36′ W.	15.0 Mi.	2.50 I.	.40 III.	II.	VIII.	X.

1934

CARIBBEAN I. WINDWARD PASSAGE TO PANAMA.—*Cont.*

#68.	2/3.	17° 3′	N.	76°30′	W.	16.7 Mi.	3.00 I. 2.00 III.
#69.	2/3.	16°33′	N.	76°27′	W.	43.6 Mi.	.24 I. .16 III. IX?
#70.	2/3(–4).	15°53′	N.	76°30′	W.	40.3 Mi.	1.20 I. 1.10 III.
#71.	2/4.	15° 2′	N.	76°39′	W.	35.7 Mi.	.10 I.
#72.	2/4–5.	14°12′	N.	76°50′	W.	67.1 Mi.	One sprig I.
#73.	2/5.	13°14′	N.	77°50′	W.	40.3 Mi.	One sprig I.
#74.	2/5.	12°50′	N.	77° 3′	W.	16.8 Mi.	.30 I. II.
#75.	2/5–6.	12° 2.5	N.	78°10′	W.	66.0 Mi.	I.
#76.	2/6.	11°17′	N.	78°45′	W.	41.5 Mi.	VIII.
#77.	2/6.	10°43′	N.	79° 6′	W.	37.1 Mi.	Fragment I.
#78.	2/7.	10°13′	N.	79°21′	W.	27.8 Mi.	No weed.

CARIBBEAN II. PANAMA TO EAST POINT OF JAMAICA.

#79.	2/14.	9°35′	N.	79°57′	W.	9.6 Mi.	One sprig III.
#80.	2/14.	9°44′	N.	80° 1′	W.	12.5 Mi.	No weed.
#81.	2/14.	10° 1′	N.	80°16′	W.	34.0 Mi.	VIII.
#82.	2/15.	10°34′	N.	80°48′	W.	56.1 Mi.	4.00 VIII.
#83.	2/15.	10°55′	N.	81°34′	W.	45.1 Mi.	.70 VIII.
#84.	2/16.	11°55′	N.	82°35′	W.	18.2 Mi.	Empty
#85.	2/16.	12° 9′	N.	82°50′	W.	11.0 Mi.	Empty
#86.	2/17.	13°23′	N.	82° 9′	W.	7.0 Mi.	Empty
#87.	2/17.	13°26′	N.	82° 0′	W.	16.4 Mi.	Empty
#88.	2/17.	13°21′	N.	81°38′	W.	26.2 Mi.	No *Sargassum.*
#89.	2/18.	13°22′	N.	81° 5′	W.	24.5 Mi.	No *Sargassum.*
#90.	2/18.	13°36′	N.	80° 8′	W.	31.0 Mi.	I. III.
#91.	2/18–19.	13°59′	N.	79°47′	W.	33.9 Mi.	Empty
#92.	2/19.	14°27′	N.	79°28′	W.	37.8 Mi.	3.75 I. .25 III. II. VIII.
#93.	2/19.	14°55′	N.	79°16′	W.	25.0 Mi.	2.10 I. .80 III. II.
#94.	2/20.	15°40′	N.	78°50′	W.	36.5 Mi.	5.50 I. .25 III. II. VIII.
#95.	2/20.	16° 8′	N.	78°39′	W.	17.8 Mi.	6.00 I. .50 III. VIII.
#96.	2/20.	16°24′	N.	78°27′	W.	20.0 Mi.	I. II.
#97.	2/21.	17° 1′	N.	78° 0′	W.	35.8 Mi.	1.50 I. 1.30 III. II. VIII.
#98.	2/21–22.	17°53′	N.	78° 0′	W.	60.5 Mi.	9.00 I. 1.60 III. II. V. VIII. IX.

CAYMAN SEA. EAST POINT OF JAMAICA TO YUCATAN CHANNEL.

#99.	2/22.	18°28′	N.	78°40′	W.	38.8 Mi.	2.00 I. 1.70 III. II. V. VIII.
#100.	2/22–23.	19°19′	N.	79°21′	W.	74.8 Mi.	2.70 I. 1.20 III. II. V. VIII.
#101.	2/23.	19°55′	N.	79°41′	W.	16.5 Mi.	1.10 I. .40 III. II. V. VIII.
#102.	2/23.	20°11′	N.	79°31′	W.	19.5 Mi.	.40 I. .40 III. II. VIII.
#103.	2/23.	20°28′	N.	79°23′	W.	19.4 Mi.	1.30 I. 2.20 III.
#104.	2/24–25.	21°15′	N.	80° 9′	W.	111.8 Mi.	I. II. III.
#105.	2/26.	19°22′	N.	81°31′	W.	19.0 Mi.	.80 I. II. III. VIII.
#106.	2/26–27.	19°11′	N.	82° 0′	W.	39.0 Mi.	7.50 I. 2.50 III. II. V. VIII.
#107.	2/27.	19° 5′	N.	82°42′	W.	28.9 Mi.	2.20 I. II. III. VIII.
#108.	2/27.	19° 2′	N.	83°20′	W.	40.6 Mi.	2.50 I. 1.50 III.
#109.	2/27–28.	19°20′	N.	83°52′	W.	29.5 Mi.	1.50 I. III.
#110.	2/28.	20° 2′	N.	83°56′	W.	39.5 Mi.	.50 I. II. III. VIII.
#111.	2/28.	21°21′	N.	84°18′	W.	42.2 Mi.	2.40 I. 1.40 III.

GULF STREAM NORTH OF MIAMI, FLORIDA.

#112.	3/8–9.	27°40′	N.	79°41′	W.	174.0*Mi.	60.00 I. 13.00 III. II. V. VIII. X.
#113.	3/9.	30° 5′	N.	79°12.5′	W.	52.4 Mi.	64.00 I. 8.20 III. 1.90 X.

* Geograph. length 240

1934

BETWEEN CAPE COD AND BERMUDA.

#114.	7/18–19.	39°47′ N.	68° 7′ W.	48.2 Mi.	1.20 I.	.55 III.	
#115.	7/19.	38°59′ N.	67°47′ W.	30.5 Mi.	Only 2 small plants altogether.		
#116.	7/19–20.	37°59′ N.	67°24′ W.	75.2 Mi.	46.50 I.	3.00 III.	
#117.	7/20.	37°33′ N.	67° 9′ W.	18.7 Mi.			
#118.	7/20.	37°19′ N.	67° 2′ W.	8.0 Mi.	4.25 I.		
#119.	7/20.	36°58′ N.	66°42′ W.	38.8 Mi.	23.75 I.	III.	
#120.	7/20–21.	36°21′ N.	65°58′ W.	62.1 Mi.			
#121.	7/22–23.	36° 3′ N.	65°52′ W.	53.5 Mi.	25.00 I.		
#122.	7/23–24.	37° 0′ N.	67°30′ W.	102.9 Mi.	15.75 I.	4.00 III.	
#123.	8/18.	40°21′ N.	69°47′ W.	59.4 Mi.	5.50 I.	2.25 III.	
#124.	8/18.	39°38′ N.	69°20′ W.	43.8 Mi.	28.75 I.	6.25 III.	
#125.	8/21.	38°29′ N.	68°54′ W.	71.6 Mi.	4.00 I.	1.50 III.	VIII.
#126.	8/21–22.	37°33′ N.	67°56′ W.	44.7 Mi.	105.00 I.	20.25 III.	
#127.	8/22.	37°17′ N.	67°31′ W.	7.2 Mi.	1.00 I.	.25 III.	
#128.	8/22.	37° 9′ N.	67°37′ W.	9.0 Mi.	43.00 I.	3.75 III.	
#129.	8/22.	36°34′ N.	67°29′ W.	61.3 Mi.	24.50 I.	2.25 III.	
#130.	8/22–23.	35°56′ N.	67°21′ W.	15.5 Mi.	5.00 I.	.25 III.	
#131.	8/26–27.	36° 4′ N.	68°12′ W.	92.3 Mi.	13.25 I.	.75 III.	
#132.	8/27.	36°53′ N.	68°58′ W.	29.1 Mi.	21.50 I.	4.25 III.	
#133.	8/27–28.	37°50′ N.	69°25′ W.	94.5 Mi.	14.50 I.	4.50 III.	
#134.	8/28.	38°46′ N.	69°49′ W.	27.6 Mi.	5.25 I.	2.25 III.	
#135.	8/28.	39°18′ N.	70° 4′ W.	41.9 Mi.	12.50 I.	9.00 III.	

1935

CAPE COD TO BERMUDA.

#136.	1/21.	38° 2.5′ N.	68°10′ W.	24.8 Mi.	1.75 I.	1.25 III.	X.
#137.	1/21–22.	37°33′ N.	68° 0′ W.	35.9 Mi.	.75 I.	1.25 III.	
#138.	1/22.	35°53′ N.	67°17′ W.	28.8 Mi.		1.75 III.	
#139.	1/23.	33°42′ N.	65°31′ W.	30.9 Mi.	1.75 I.	6.50 III.	
#140.	1/23.	33° 7.5′ N.	65° 2.5′ W.	49.9 Mi.	4.75 I.	14.50 III.	II.

SARGASSO SEA. BERMUDA TO TURKS ISLAND.

#141.	2/6.	29°56′ N.	65°55′ W.	17.65 Mi.	13.75 I.	7.25 III.	1.00 II.	VIII.	X·	
#142.	2/6.	29°38′ N.	66° 4′ W.	21.5 Mi.	22.00 I.	11.00 III.	4.00 II-VIII.	V.	1.00 X.	
#143.	2/6.	29° 6′ N.	66°23′ W.	44.8 Mi.	12.00 I.	11.00 III.	1.50 II.	2.00 X.	VIII.	
#144.	2/7.	28°30′ N.	66°41′ W.	25.0 Mi.	16.50 I.	87.20 III.	II.	1.50 X.	VIII.	
#145.	2/7.	28° 3′ N.	66°56′ W.	28.6 Mi.	18.00 I.	10.00 III.	1.50 X.	1.50II.	VIII.	V.
#146.	2/7.	27°35′ N.	67°17′ W.	33.1 Mi.	16.00 I.	12.00 III.	3.50 II.	5.50 X.	VIII.	
#147.	2/7.	26°57′ N.	67°44′ W.	55.5 Mi.	47.00 I.	21.00 III.	5.00 II.	6.50 X.		
#148.	2/8.	26°11′ N.	68°10′ W.	46.0 Mi.	29.00 I.	12.00 III.	3.50 II.	3.50 X.		
#149.	2/8.	25°37′ N.	68°25′ W.	29.4 Mi.	19.00 I.	2.50 X.	II.			
#150.	2/8.	24°55′ N.	68°42′ W.	17.3 Mi.	54.00 I.	7.5 III.	2.25 II.	6.00 X.	IX.	
#151.*	2/8–9.	24°35′ N.	68°54′ W.	24.3 Mi.	37.50 I.	9.00 III.	1.50 II.	4.00 X.		
#152.	2/9.	23°58.5′ N.	69°27′ W.	39.5 Mi.	88.00 I.	35.00 III.	3.00 II.	17.50 X.	VIII.	IX?
#153.	2/9.	23°31.5′ N.	69°45′ W.	23.3 Mi.	23.00 I.	7.00 III.	2.00 II.	1.50 X.	VIII.	
#154.	2/9.	22°56′ N.	70°13′ W.	58.4 Mi.	17.00 I.	2.75 III.	1.25 II.	1.50 X.		
#155.	2/10.	22° 4′ N.	70°40′ W.	57.9 Mi.	10.50 I.	15.00 III.	2.00 X.	II.	VIII.	

TURKS ISLAND TO WINDWARD PASSAGE.

#156.	2/10.	21°17.5′ N.	71°15′ W.	49.4 Mi.	8.25 I.	2.50 III.	1.25 X.		
#157.	2/10–11.	20°30′ N.	72°46.5′ W.	92.3 Mi.	14.00 I.	4.00 III.	II.	VIII.	X.

---

* For account of subsurface nets used at this station see page 10.

1935

CAYMAN SEA. WINDWARD PASSAGE TO YUCATAN CHANNEL.

#158.	2/11–12.	19°57′ N.	74°14′ W.	69.3 Mi.	4.25 I. III. II. VIII. IX. X.
#159.	2/12–13.	19°24′ N.	76°30′ W.	172.6 Mi.	1.72 I. 4.20 III + X. .28 VIII. II.
#160.	2/13.	19°20′ N.	78°37′ W.	47.3 Mi.	1.10 I. 3.60 III + X. .62 VIII. .15 II. .30 IX.
#161.	2/13–14.	19°34′ N.	80°11′ W.	116.1 Mi.	1.70 I. 4.00 III + X. .40 VIII. II.
#162.	2/14.	19°53′ N.	81°54′ W.	67.9 Mi.	.80 I. 2.20 III + X. 2.20 VIII. II. 1.32 IX.
#163.	2/14–15.	20°27′ N.	83° 2′ W.	78.5 Mi.	2.00 lb. Total haul. Details not available.
#164.	2/15.	21°12.5′ N.	84°20′ W.	89.0 Mi.	.38 I. .81 III. 1.10 VIII. IX.

GULF OF MEXICO I. SOUTHEASTERN REGION BETWEEN YUCATAN BANK AND STRAITS OF FLORIDA.

#165.	2/16–17.	22°15′ N.	86°52′ W.	73.3 Mi.	No pelagic weeds.
#166.	2/18.	24°15′ N.	85°51′ W.	24.4 Mi.	.20 I. .75 III. .10 VIII. II.
#167.	2/18–19.	23°49′ N.	84°16′ W.	143.5 Mi.	.40 I. 1.30 III. .20 VIII.

GULF OF MEXICO II. NORTHERN GULF.

#168.	3/5–6.	27°32′ N.	88°21′ W.	50.4 Mi.	4.50 I + III + VIII.
#169.	3/6.	26°55′ N.	88°21′ W.	40.9 Mi.	4.00 I + III + VIII.
#170.	3/6.	26°23′ N.	88°12′ W.	48.7 Mi.	33.50 I. Fragments III. VIII.
#171.	3/6.	25°54.5′ N.	88°18′ W.	1.4 Mi.	I. VIII.
#172.	3/7.	25°43′ N.	88°23′ W.	10.9 Mi.	17.25 I. III. .50 VIII.
#173.	3/25.	28° 8′ N.	89°24′ W.	68.9 Mi.	45.25 I. 1.85 III. 1.90 VIII.
#174.	3/25–26.	27°30′ N.	89°47′ W.	35.5 Mi.	26.50 I. .95 III. 2.80 VIII.
#175.	3/26.	27°33′ N.	89°53′ W.	18.4 Mi.	17.00 I. 1.40 III. .35 VIII.
#176.	3/26.	27°57.5′ N.	89°53′ W.	21.9 Mi.	14.50 I. .50 III. .50 VIII.
#177.	3/26.	28°22.5′ N.	89°50′ W.	21.3 Mi.	12.25 I. .25 III. .50 VIII.
#178.	3/27.	c.28°45′ N.	c.89°50′ W.	42.3 Mi.	60.75 I. 4.50 III. 4.50 VIII.
#179.	3/27.	28°21′ N.	90°18′ W.	41.9 Mi.	33.75 I. 3.00 III. 3.00 VIII.
#180.	3/27–28.	27°40′ N.	91°24′ W.	92.3 Mi.	64.00 I. 11.75 III. + VIII.
#181.	3/28.	27°25′ N.	92°12′ W.	30.5 Mi.	11.00 I. .75 III. 1.00 VIII.
#182.	3/29.	c.29° 7′ N.	92°41′ W.	27.6 Mi.	30.50 I. 2.75 III. 8.25 VIII.
#183.	3/29.	29° 7′ N.	93°19′ W.	40.2 Mi.	18.75 I. 4.90 III. 1.60 VIII. X.
#184.	3/31–4/1.	27°41′ N.	96°26′ W.	54.2 Mi.	27.50 I. 4.50 III. 3.00 VIII. X.
#185.	4/1.	27°15′ N.	96°30′ W.	14.4 Mi.	6.75 I. 2.00 III. .25 VIII.
#186.	4/2–3.	25°57′ N.	94°44′ W.	62.4 Mi.	13.00 I. 1.20 III. 4.80 VIII.
#187.	4/3–4.	c.25°12′ N.	c.94°6′ W.	64.1 Mi.	13.50 I. .80 III. 1.20 VIII.

GULF OF MEXICO III. YUCATAN BANK.

#188.	4/8–9.	24° 5′ N.	87°57′ W.	58.8 Mi.	I. VIII.

GULF OF MEXICO IV. FLORIDA BANK.

#189.	4/11–12.	25°48′ N.	84° 5′ W.	86.4 Mi.	5.25 I. .60 III. .40 VIII. II.
#190.	4/12.	24°36′ N.	83° 2′ W.	46.0 Mi.	4.25 I. 1.30 III. .45 VIII.

STRAITS OF FLORIDA.

#191.	4/13.	23°41′ N.	81°52′ W.	77.7 Mi.	1.25 I. 1.75 III. II. VIII.
#192.	4/13–14.	24°42′ N.	80°33′ W.	59.4 Mi.	1.00 I. III. II. VIII.

GULF STREAM NORTH OF MIAMI, FLORIDA.

#193.	4/19–20.	28°10′ N.	79°42.5′ W.	135.3 Mi.	7.50 I. 6.50 III. + VIII
#194.	4/20.	30°24′ N.	79°25′ W.	51.5 Mi.	3.75 I. 3.25 III. 1.00 VIII. X

SUMMARY

The frame and net of a collecting apparatus specially designed to gather floating weeds from the sea surface on a quantitative basis is described, and the method of operation discussed (pp. 4–8).

It is pointed out that this collector has been in actual operation in the surface of the Sargasso Sea and of the Central American Seas for a total cumulative towing length of nearly 7,000 nautical miles, and that as a result of this towing more than 4,700 pounds of pelagic weeds have been sorted and weighed on board (pp. 3–4).

An account is given of experiments confirming the lack of vertical dispersal of pelagic *Sargassum* weeds (pp. 8–10).

The taxonomy of the pelagic *Sargassum* weeds is discussed in a preliminary fashion, with a practical key for their identification, and a descriptive atlas of herbarium silhouettes. A non-binominal, purely descriptive classification of the dominant forms is used as a basis for comparisons and discussions of distributions. The opinion is expressed that the fixed, more or less distinct external forms in which the truly pelagic weeds occur, probably represent only phenotypic variations of not more than two separate species, *S. natans* and *S. fluitans*. It is further pointed out that even the distinctness of these two species, although apparently most probable, cannot as yet be considered to be established entirely beyond all doubt (pp. 11–51).

A fertile plant attached to a drifting piece of wood (mangroove root ?), but otherwise indistinguishable from sterile representatives of the pelagic *S. fluitans*, is described (pp. 49–51).

The quantitative distribution of the dominant pelagic weeds is described (pp. 51–68). It is pointed out that the floating vegetation in the Caribbean and Cayman Seas is always very sparse, and that it is virtually completely absent from the entire southern half of the Caribbean itself. In the northwestern region of the Gulf of Mexico, however, a secondary accumulation of apparently deteriorating weeds in considerable abundance was observed over a wide area. At least during the winter period in which observations were made these weeds were obviously in a very poor condition and on the average extremely heavily overgrown by epizoan incrustations (pp. 54–58).

The main region of occurrence of thriving pelagic weeds was found to be entirely outside the Central American Seas in that part of the open North Atlantic designated as the Sargasso Sea. Observations in the western Sargasso Sea during three separate cruises with a total towing-length of over 1300 nautical miles indicate an abundance of pelagic weeds, varying in the records for the three years between about two and somewhat more than five metric tons wet weight per square nautical mile. If these figures are representative of the entire Sargasso Sea, the total pelagic vegetation might be estimated at four to ten million metric tons. It is suggested that this may be accepted as a usable

statement of the order of magnitude of the total pelagic *Sargassum* vegetation of the North Atlantic (pp. 54–58).

Annual fluctuations in the relative frequencies of the two predominant types of pelagic weeds, *S. natans I* and *S. fluitans III*, are pointed out (pp. 59–64), and the distribution of the less abundant pelagic forms is discussed separately (pp. 65–67). It is shown that the distribution of the broadleaved *S. natans VIII* differs fundamentally from that of all other pelagic *Sargassa* in that it has its maximum abundance within the Central American Seas and not in the open Atlantic (p. 66).

By a process of elimination on the principle of *reductio ad absurdum*, it is concluded that there is no conceivable source and process of annual renewal of pelagic *Sargassum* vegetation from benthonic flora which could possibly maintain the floating vegetation in its observed abundance with an average duration of the pelagic state of the individual plants to be reckoned in less than decades (pp. 68–84).

The distribution of the pelagic *Sargassum* weeds confirms previous hydrographic conclusions on two points. 1) The failure of the drifting flora to penetrate southward across the Caribbean agrees with the assumption that the Caribbean surface water is mainly derived from the SE *via* the North Equatorial Current and not from the Sargasso Sea itself (p. 54). 2) The accumulation of floating weeds in the northwestern part of the Gulf of Mexico must be interpreted as a result of pure wind drift, due to prevailing easterly winds, moving the weeds in relation to the water, and this accumulation could scarcely take place in the presence of a significant tendency to outward movement of the surface water itself towards the Straits of Florida (p. 56).

MAIN SOURCES TO WHICH REFERENCE HAS BEEN MADE IN THIS REPORT

Since it does not seem necessary in this connection to print the entire bibliography of the earlier literature already reviewed by Winge (1923), only the sources which have been of main usefulness for direct reference in the preparation of this report are listed herewith for the reader's convenience, together with such references as did not come within the scope of Winge's discussion. The latter should be consulted for any author or title not mentioned in the following.

ANTZE, G.
1901. Revision der Oberflächenströmungen des Nordatlantischen Ozeans. Inaugural Dissertation. Minden i. W. 1901.

ATKINS, W. R. G.
1923. The phosphate content in fresh and salt waters in its relationship to the growth of the Algal plankton. Journ. Mar. Biol. Assoc. Vol. XIII, No. 1.

Börgesen, F.

1914a. The species of Sargassum found along the coast of the Danish West Indies. Mindeskrift f. japetus steenstrup. Copenhagen 1914.

1914b. The marine algae of the Danish West Indies. Pt. 2. Phaeophyceae. Dansk Botanisk Arkiv. Vol. 2, No. 2. Copenhagen 1914.

Collins, F. S. and Hervey, A. B.

1917. The algae of Bermuda. Proc. Amer. Ac. Art. Sci. Boston, Vol. 53, No. 1.

Cooper, L. H. N.

1933. Chemical constituents of biological importance in the English Channel. Journ. Mar. Biol. Assoc. Vol. XVIII, No. 2.

1934. The variations in excess base with depth in the English Channel with reference to the seasonal consumption of calcium by plankton. Journ. Mar. Biol. Assoc. Vol. XIX, No. 2.

Howe, M. A.

1918. Algae. In N. L. Britton: Flora of Bermuda. Charles Scribner, New York, 1918.

1920. Algae. In N. L. Britton and C. F. Millspaugh: The Bahaman Flora. Published by the authors. New York, 1920.

Krümmel, O.

1891. Die nord-atlantische Sargasso-See. Petermanns Mittheilungen. Vol. 37, 1891, pp. 129–141, Plate 9.

Murray, T. and Hjort, T.

1912. The depths of the Ocean. Macmillan and Co. London 1912.

Nielsen, J. N.

1925. Golfströmmen. Geografisk Tidskrift. Bd. 28, Hefte 1. Copenhagen, 1925.

Parr, A. E.

1935. Report on hydrographic observations in the Gulf of Mexico. Bull. Bingham Oceanogr. Coll. Vol. V, Art. 1. New Haven, Conn., 1935.

1937. A contribution to the hydrography of the Caribbean and Cayman Seas. Bull. Bingham Oceanogr. Coll. Vol. V, Art. 4. New Haven, Conn., 1937.

Seiwell, H. R.

1935. The annual organic production and nutrient phosphorus requirement in the tropical western north Atlantic. Journal du Conseil. Vol X, No. 1. Copenhagen, 1935.

Schmidt, Johs.

1933. Danish eel investigations during 25 years. Carlsberg Foundation. Copenhagen, 1933.

Taylor, Wm. R.

1928. The marine algae of Florida. Carnegie Inst. of Washington Publ. No. 379. (Pap. Tortugas Lab. Vol. XXV.)

TILDEN, J. E.
1935. The algae and their life relations.

WINGE, Ö.
1923. The Sargasso Sea, its boundaries and vegetation. Rep. Danish Oceanogr. Exp. 1908–10. Vol. III. Misc. Pap. No. 2. Copenhagen, 1923.

Contribution No. 236

Reprinted from Ecology, Vol. 20, No. 4, October, 1939
Printed in U. S. A.

VARIATION IN THE TRANSPARENCY OF THREE AREAS OF THE ATLANTIC THROUGHOUT THE YEAR

George L. Clarke

Biological Laboratory, Harvard University,
and
Woods Hole Oceanographic Institution[1]

Our previous measurements of the penetration of daylight into the western North Atlantic Ocean have revealed striking differences in the transparency of the water and hence in the intensity of the illumination to which aquatic animals and plants are subjected (Clarke, '36, '39). However, these observations of light penetration have been confined to the summer months except for a series of observations made throughout the year at the western entrance of Vineyard Sound off Woods Hole (Clarke, '38). In the latter investigation a seasonal fluctuation in transparency of considerable magnitude was found and calculations showed that these variations must result in such large differences in the intensity of the light which reached organisms on the bottom or at mid-depths as to be of great ecological significance. In the study of the biology of the other oceanic areas, it was therefore important not only to compare the transparencies of the several regions at other seasons, but also to ascertain the magnitude of the changes in illumination which would be experienced during the year at one point.[2]

To this end measurements of light penetration were undertaken from the research vessel " Atlantis " on her nine cruises between Montauk Point, Long Island, N. Y., and Bermuda, from October 1937 to November 1938. On these cruises three areas of the ocean were traversed each characterized by a distinct type of water, and a standard station was established in each (Fig. 1): Station A in the *coastal water* which overlies the continental shelf; Station B in the *" slope " water* which extends between the continental slope and the Gulf Stream; and Station C in the *Sargasso water* which fills the whole of the central North Atlantic and of which the Gulf Stream is the western and northern edge. The three areas are of interest biologically because of the extreme contrast which they present. The plankton in the coastal water is abundant but composed of relatively few species. The Sargasso Sea is extremely barren in respect to plankton, although the number of species represented is large. The slope water is a zone of mixing between the other two areas. Bottom

---

[1] Contribution No. 236.

[2] The significance which variations in transparency would have for the photic reactions of animals living at great depths has been discussed elsewhere (Waterman, Nunnemacher, Chace and Clarke, '39).

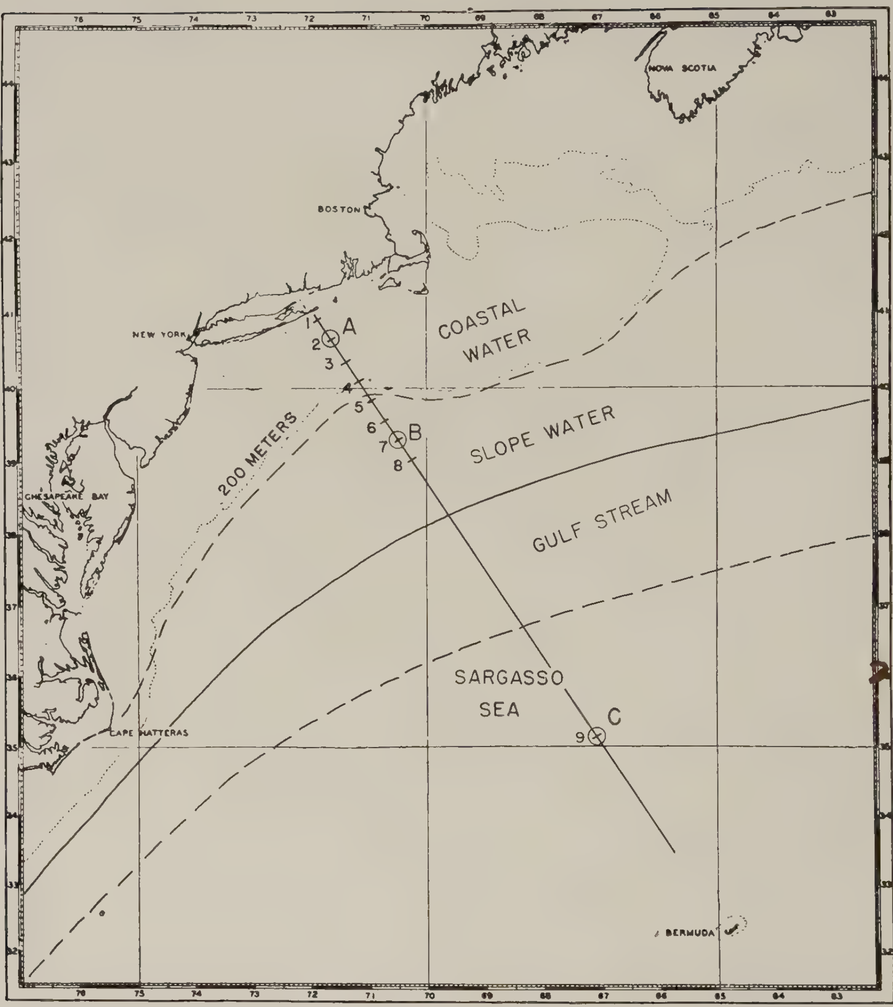

NOVA SCOTIA
BOSTON
NEW YORK
CHESAPEAKE BAY
CAPE HATTERAS
BERMUDA
COASTAL WATER
SLOPE WATER
GULF STREAM
SARGASSO SEA
200 METERS
A
B
C
1
2
3
4
5
6
7
8
9
76
75
74
73
72
71
70
69
68
67
66
65
64
63

FIG. 1. Chart showing the areas in the Atlantic in which observations were made. The sharply delineated boundary of the Gulf Stream toward the coast is represented by a solid line; the more indefinite boundary toward Bermuda is indicated by a broken line.

fauna is much richer on the continental shelf than in deep water. Successful commercial fishing is limited almost entirely to the coastal region.

Apparatus and Procedure

The measurements were made with two emission photocells of the Photronic type manufactured by the Weston Electrical Instrument Corporation. One of these was hung in gimbals and exposed on deck to the sun and sky; the other was placed in a watertight case provided with a plate glass window 10 cm. in diameter and lowered into the sea. The current generated by the cell was measured by a Westinghouse Microammeter with full scale deflection of 25 μa and a shunt for larger currents. Diffusing discs of flashed opal glass were used over the receiving windows of both the deck cell and the sea cell for all measurements. When used in full sunlight, the effective area of the window was reduced by placing a diaphragm with hole about 1.7 cm. in diameter over the diffusing disc. The intensities to which the cells were exposed were thus limited and the curvature of the response of our instruments within this restricted range was determined by comparison with a caesium photoelectric cell whose response was known to be linear (Powell & Clarke, '36).

The spectral sensitivity of the Photronic cell exhibits a maximum at 5800 A and drops off to 10 per cent of the maximum at 7080 A and at 3420 A. Thus without a color filter the photometer was sensitivity to the total visible spectrum. At each station the photometers were used without filters for one series of measurements, and in as many cases as possible, a second series was undertaken in which the light reaching the instrument was confined chiefly within the green region of the spectrum. This was accomplished by placing beneath the diffusing discs of both photometers a Schott-Jena filter of type VG–2[3] (practically identical to type VG–9). The transmission of this filter reaches a maximum at 5300 A and drops off to 10 per cent of the maximum at about 6200 A and 4600 A. The point of maximum sensitivity of the combination of cell plus filter can safely be taken as about 5500 A and thus corresponds closely to the spectral sensitivity of the human eye.

The measurements at sea were carried out by Mr. Dean F. Bumpus, Biological Technician for the Woods Hole Oceanographic Institution. The ship was first hove to with her stern directed toward the sun, and the submarine photometer was suspended from the end of the mizzen boom. The shadow of the ship's hull was thus avoided.

Changes in the temperature of the Photronic cells, which had been found to affect the emission of the instruments (Waterman, Nunnemacher, Chace and Clarke, '39), were reduced to a minimum by lowering the submarine photometer into the water and placing the deck photometer in position long enough before measurements were begun for them to come into thermal equilibrium with the water and air respectively.

The submarine photometer was raised to a point just about the surface for the first measurement and its emission compared with that of the deck photometer. The observed ratio was taken as 100 per cent. The submarine photometer was then lowered successively to depths of 2,[4] 6, 10 m., every

---

[3] In four of the earliest measurements Schott-Jena filters BG–18 and GG–11 were used together instead of VG–2. This combination allows essentially the same transmission. Series 467, which was made with BG–18 and GG–11 and series 468, made with VG–2 and carried out immediately afterwards at Station B yielded almost identical curves for light penetration.

[4] When possible a measurement was made also at 1 m., but the action of the waves

TABLE I. *Summary of measurements of light penetration and comparison of extinction coefficients for the total visible light and for the green component of daylight*

Date	Atlantis Station	Weather	Sea	Wind	No Filter					Green Filter				
					Series	Range in m.	*k*, Average extinction coefficient	Per cent average absorption per meter	Per cent surface light at 2 m.	Series	Range in m.	*k*, Average extinction coefficient	Per cent average absorption per meter	Per cent surface light at 2 m.
Station A—Coastal Water														
Oct. 2, '37	2904	BC–C	3	3	452	1–48	.14	13	45	453*	1–38	.12	11	60
May 17, '38	3038	B	2	3	464	1–54	.11	10	59					
May 18, '38	3041	O	2	3	465	2–54	.12	11	66	465A*	2–20	.11	10	70
July 17, '38	3111	O Fog	1	1	477	2–60	.14	13	65	478	2–44	.13	12	74
Sept. 3, '38	3153	BC	1	1	485	2–60	.11	10	70	486	2–50	.11	10	80
Sept. 29, '38	3157	C Fog	1	2	487	1–40	.15	14	66	488	1–25	.17	16	69
Nov. 3, '38	3215	BC	1	1						494†	1–25	.16	15	—
Station B—Slope Water														
Oct. 5, '37	2912	BC–C	3	3	454	1–76	.065	6.5	70					
Jan. 4, '38	2943	BC	2	1	457	1–107	.050	5.0	79					
Apr. 12, '38	3031	B	3	3	462	2–49	.10	10.	63	463*	2–20	.11	10	70
June 1, '38	3052‡	B	1	1	466	1–110	.065	6.5	64	467*	2–70	.079	7.9	71
June 1, '38	3052‡	B	1	1						468	2–65	.077	7.7	65
July 14, '38	3105	B	5	5	475	4–121	.058	5.8	—	476	4–74	.062	6.2	—
Sept. 1, '38	3149	C	2	2	484	2–101	.066	6.6	82	483	2–59	.071	7.1	75
Nov. 2, '38	3212	B	2	2	493†	2–70	.096	9.6	73	492†	2–50	.087	8.7	71
Station C—Sargasso Water														
Oct. 9, '37	2924	C	3–4	2–3	455	2–129	.042	4.2	63					
Dec. 10, '37	2931	C	1	1	456	2–120	.047	4.7	78					
Jan. 7, '38	2945	BC	2	2	458	2–91	.059	5.9	74					
Apr. 7, '38	3025	R.Q.O.	1	1	461	2–59	.066	6.6	51?					
June 5, '38	3062	B	4	3	469	2–135	.051	5.1	68	470	2–90	.059	5.9	74
July 9, '38	3093	BC	1	1	471	5–131	.054	5.4	—					
July 10, '38	3093	BC	2	2	474	2–131	.053	5.3	70	473	2–94	.056	5.6	63
Aug. 29, '38	3147	C	2–3	2–3	481	2–113	.044	4.4	48?	482	2–78	.048	4.8	70
Oct. 7, '38	3174§	C	1	1	489	1–127	.047	4.7	73					
Oct. 27, '38	3200	BC	1	1						491†	2–50	.066	6.6	82

* Measurement made with Schott-Jena filters BG–18 and GG–11. Filter VG–2 used for all others in this column.
† Measurement made with Westinghouse "Photox" cell.
‡ Observation made 70 miles SE of Station B.
§ Observation made 13 miles NW of Station C.

5 m. to 30 m., every 10 m. to 60 m. and every 15 m. to the greatest depth at which a reading could be obtained. The "corrected" vertical depth of each reading was obtained by multiplying the length of the supporting cable by the cosine of the angle which it made with the vertical as it entered the water. The value obtained at each depth was corrected for the curvature in the emission of the cell and calculated as a percentage of the light reaching the surface of the sea. Since both the submarine photometer and the deck photometer were read for each depth, every measurement is independent of the others and therefore the average transparency for the whole series at each station is a highly reliable value.

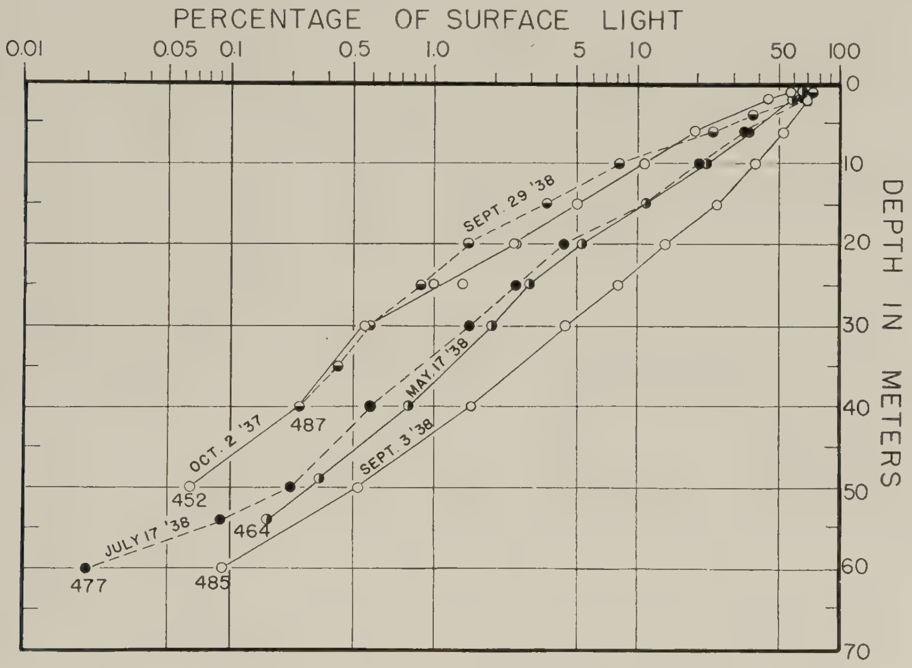


FIG. 2. Coastal Area—Station A. Relation between depth and total visible light (photometer without filter) expressed as a percentage of the light just over the surface (logarithmic scale). Series number indicated at the end of each curve (see Table I for data).

The apparatus and procedure conform to the recommendations of the Subcommittee on Light Measurements of the International Council for the Exploration of the Sea (Atkins, Clarke, Pettersson, Poole, Utterback and Angstrom, '38).

OBSERVATIONS

The observations of light penetration in the three areas under consideration are summarized in Table I and a large number of the individual series

---

rendered readings near the surface highly inaccurate and occasionally reliable measurements could not be obtained short of 6 m.

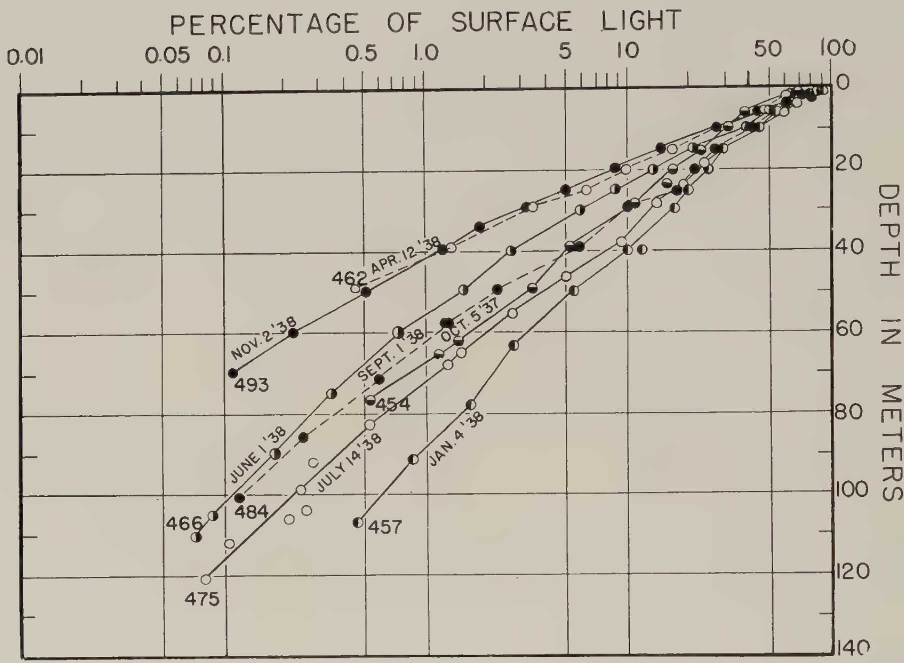


FIG. 3. Slope water—Station B. Relation between depth and total visible light (photometer without filter) expressed as a percentage of the light just over the surface (logarithmic scale). Series number indicated at the end of each curve (see Table I for data).

of measurements are presented graphically in figures 2, 3, and 4. It will be observed that in spite of variable sea and sky conditions readings which make up each series are consistent and for the most part fall on a remarkably straight line in a semi-logarithmic plot. The water is thus known in most cases to have been highly homogeneous optically over the range studied. Consequently it is legitimate in comparing one series of measurements with another to use the *average* value of the extinction coefficient [5] or the average percentage absorption per meter.

The extinction coefficients for the measurements of the total visible spectrum made with no color filter over the photometers are seen from Table I to be closely followed for depths greater than 2 m. by the values for the green component of daylight only (see also Fig. 6). This parallelism may be explained by the rapid absorption of the light at the two ends of the spectrum by the first few meters of water with the result that in the deeper strata the light is largely confined to the central part of the spectrum. The remaining light

---

[5] The extinction coefficient is defined as k in the equation $\frac{I}{I_0} = e^{-kL}$ where the intensity of the light is reduced from I_0 to I in the depth L expressed in meters. See Whitney ('39) for a more elaborate form of this equation.

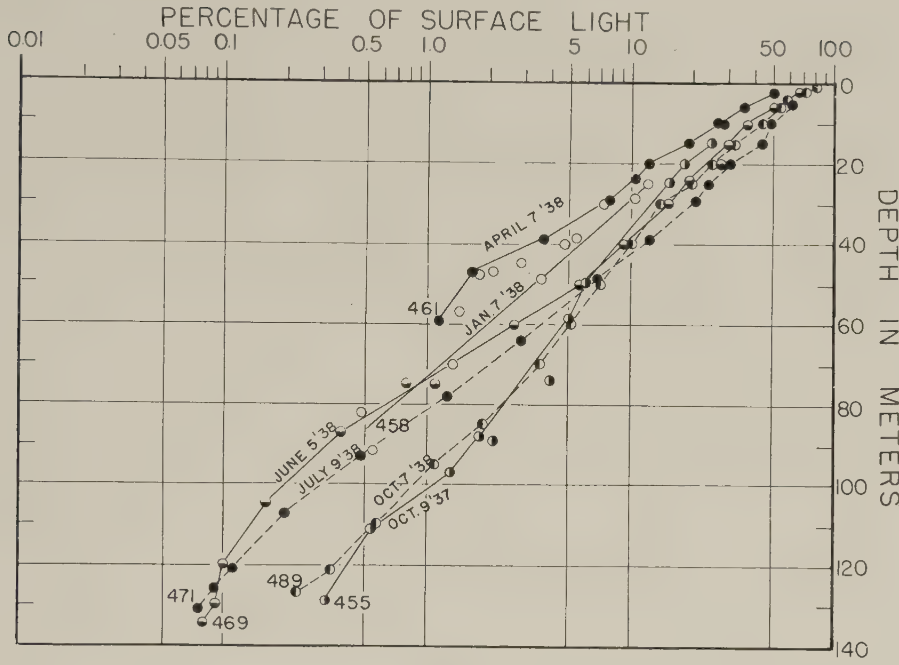


FIG. 4. Sargasso Sea—Station C. Relation between depth and total visible light (photometer without filter) expressed as a percentage of the light just over the surface (logarithmic scale). Series number indicated at the end of each curve (see Table I for data).

would therefore exert the same effect on the photometer whether used with or without the green filter. This explanation is borne out by a comparison of the percentage of the surface light which was observed to remain at a depth of 2 m. in the two cases (Table I). In practically every instance the photometer measuring the total light (no filter) indicated a greater reduction at 2 m. than was the case when the instrument was limited to the green component. For a detailed study of the seasonal and regional differences in general transparency below 2 m. either set of data may be used and the two sets serve as a check on each other. Actually the measurements with no filter will be considered below since we have more of these series.

Coastal Water—Station A

The measurements at Station A extended nearly to the bottom which varied in depth between 63 m. and 75 m. The water exhibited a rather uniform transparency at all depths on every occasion that the station was visited. Slight but definite changes in the slope of the curves occurred at 20 m. on September 29, 1938, and at 30 m. on October 2, 1937, and these differences in transparency were encountered at exactly the same depths in the succeeding measurements with the green filter. The indicated changes in rate of light penetration are therefore real and not due to instrumental or observational errors. The water in this region becomes very highly stabilized during the summer and early autumn months because of thermal stratification. (For example, on July 17th the temperature changed abruptly from 20° C. at 10 m. to 7° C. at 35 m.) Under such circumstances the water is not easily mixed and material influencing absorption can accumulate locally (Pettersson, '34; Oster and Clarke, '35; and Whitney, '38). Although we have no information in the present case as to the precise agent responsible, a similar explanation undoubtedly accounts for the changes in transparency with depth.

Throughout the period of observation the average absorption per meter at this station varied from a maximum of 14 per cent (extinction coefficient, $k = .15$) on September 29, 1938, to a minimum of 10 per cent ($k = .11$) on September 3, 1938, and May 17, 1938. There appears to be no particular seasonal trend in the changes of transparency, but irregular fluctuation would be expected in the water at this station which is subject to so many disturbing influences. The strength of the wind, the stability of the water, and the abundance of plankton and its derivatives all vary widely. At times when stirring by wind, tides, or currents is effective, the nearness of the shore and of the bottom makes it possible for obscuring material to be introduced rapidly into the water. Consistent with this view is the fact that the seasonal variations in transparency at Station A are not as great as those observed by Clarke ('38) for a station off the western entrance to Vineyard Sound—a location also to be included in the "coastal area," but much closer to shore. The transparency of the water at Station A at all times corresponded to the lower absorption values observed off Vineyard Sound.

Slope Water—Station B

Since Station B was located some distance beyond the edge of the continental shelf the depth of the water was very much greater (about 2600 m.), and although the light penetration observations extended to a maximum of 121 m., the stratum measured represents only a small fraction of the total depth. The curves for the individual series (Fig. 3) are all relatively straight, indicating homogeneous water, although slight changes in slope are to be observed as for example in the measurement of October 5, 1937. The absorption of light at this station varied from a maximum of 10 per cent per meter ($k = .10$) on April 12, 1938, to a minimum of 5 per cent per meter ($k = .050$) on January 4, 1938.

This relatively great fluctuation in the clearness of the water would appear strange for a location in deep water well removed from the shore if it were not for the fact that the slope water has been shown to be a region of extensive mixing (Iselin, '36). Eddies of the clearer Sargasso water tend to be ejected from the western edge of the Gulf Stream and to mix with eddies of the more turbid coastal water which have drifted out from the continental shelf. In the intervening region of slope water patches containing a high percentage of Sargasso water or of coastal water might thus be expected to occur before mixing became complete. This suggestion is well substantiated by figure 5 in which salinity is plotted against depth (for the upper 300 m.) for the several occasions on which Station B was visited.[6] On January 4, 1938, almost pure Sargasso water was present, as is shown by the occurrence of salinities higher than 36.0 per cent. The unusually high transparency on that date is thus directly explained. On the other hand, the low salinities which obtained on April 12, 1938, and, in the upper strata, on November 1, 1938, indicate a considerable admixture of coastal water and account for the less effective penetration of light. On October 5, 1937, an exceedingly abrupt change in salinity was encountered at about 20 m., and although the depth of the transition does not correspond exactly to the change in slope of the light intensity curve, one observes that the uppermost water layer was less transparent on this date than on any other occasion. Salinities and transparencies of intermediate values were encountered on the remaining visits to this station.

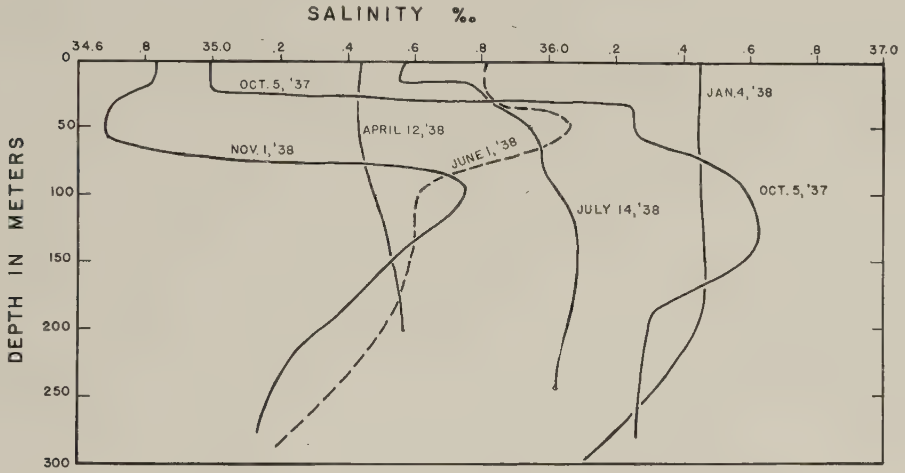


FIG. 5. Relation between depth and salinity in the slope water (Station B).

Sargasso Water—Station C

At Station C the water was sufficiently clear to allow measurements to be extended to a maximum depth of 135 m., but since the bottom here was at about 5200 m., the illuminated stratum was an even smaller fraction of the total depth than at Station B. Although the water appeared to be optically homogeneous because of the essential straightness of the curves (Fig. 4), the individual measurements were somewhat irregular due in part to adverse

---

[6] I am indebted to Mr. C. O. Iselin for this information.

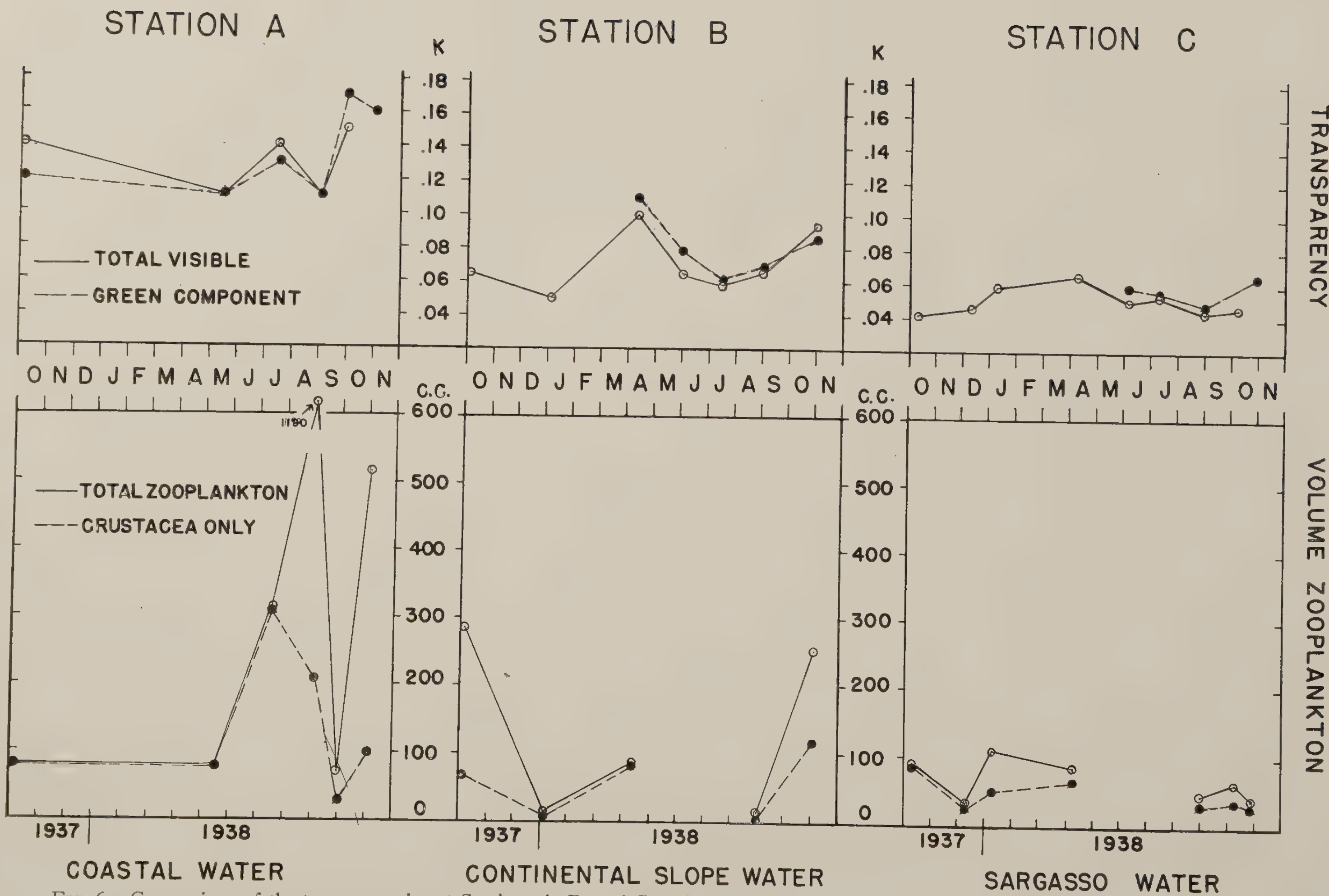


FIG. 6. Comparison of the transparencies at Stations A, B, and C, and the abundance of zooplankton. The months of the year are indicated between the graphs. Transparency—variation in value of extinction coefficient, *k*. Zooplankton—volume as measured by displacement of catches with a scrim net, 75 cm. in diameter, calculated on the basis of a one-hour oblique haul from 50–0 m. (Station A) or from 100–0 m. (Stations B and C).

weather and in part to the greater error in estimating the exact vertical depth with longer lengths of wire out. The absorption of light varied from a maximum of 6.6 per cent per meter ($k = .066$) on April 7, 1938, to a minimum of 4.2 per cent per meter ($k = .042$) on October 9, 1937. The slight differences in transparency observed are probably not assignable to any one of the environmental factors, all of which are usually highly constant in this area. The salinity at every depth down to 300 m. was confined between values of 36.1 and 36.7 on all occasions. The temperature at the surface varied only between 20° and 27° C., and at 100 m. it ranged between 18° and 23° C. In neither case was correlation with transparency observed.

DISCUSSION

A comparison of the three areas throughout the year shows that in spite of the variations in transparency at each station, the absorption rates in the several regions overlap to only a slight extent (Fig. 6). The average values for each differ distinctly and allow the general conclusion to be reached that the Sargasso water is the most transparent, that the coastal water is much less clear, and that the slope water is intermediate (Table II).

TABLE II. *Comparison of average absorption and of absolute and relative variation in the three areas*

Area	Absorption per meter		
	Range	Average	Relative variation
	Per cent	*Per cent*	*Per cent*
Coastal water	10–14	12 ($k = .13$)	33
Slope water	5–10	7.1 ($k = .071$)	70
Sargasso water	4.2–6.6	5.1 ($k = .051$)	47

The slope water exhibits the greatest absolute variation and also the greatest variation relative to the value of the average absorption. The absolute variation in the coastal water is somewhat less and in the Sargasso water is very much smaller than in the slope water. The *relative* variation of the coastal water, however, turns out to be somewhat less than the *relative* variation of the Sargasso water because of the high values for the absorption of the coastal water. The fluctuations in the transparency of the Sargasso water, the absorption of which is nearly as low as that of distilled water (Clarke and James, '39), would be accounted for by extremely slight changes in the amount of absorbing material present. For the variations observed in the coastal water the addition or removal of much larger amounts of obscuring matter would be required.

These differences in the average values of transparency and in the amount of variability have been shown above to correspond to important differences in the hydrography of the areas. But differences in the temperature and salinity of the water do not themselves influence transparency significantly; they merely indicate the derivation of the body of water in which the measurement was made. Thus we have seen that the water at Station C was at all times typical of the Sargasso Sea area, the water at Station A exhibited the variability characteristic of the coastal area, and the water at Station B was on some occasions similar to coastal water and on some occasions was nearly identical to Sargasso water. Our ultimate problem, therefore, is to determine the cause of the difference between the transparency of Sargasso water and of coastal water and to explain the greater variation in the amount of obscuring material in the latter.

The high transparency of the Sargasso Sea is due in part to the long interval since the water in that area has been in contact with the bottom or with the shore, and the consequent opportunity for mud particles to settle out, and in part to the paucity of the plankton (Fig. 6). In the coastal area detritus is introduced from the shore wherever wave action or tidal turbulence is strong or rivers debouch and from the bottom whenever vertical stirring is sufficiently effective to reach the bottom, as it is on the continental shelf during the winter months. In addition the plankton is abundant and extremely variable in the coastal water, as is apparent from figure 6 (see also Bigelow and Sears, '39).

A close scrutiny of figure 6 shows, however, that no exact correlation is indicated between the abundance of the total zooplankton, or of the crustacea, and the changes in transparency. No hauls were made at these stations specifically for the quantitative study of the phytoplankton, but diatom material was found in the zooplankton nets during periods of flowering. None of these occurrences corresponded to the high values for the extinction coefficient. On May 17, 1938, at Station A, the transparency ($k = .115$) was practically identical to the value observed on May 18, 1938 ($k = .116$), at a station only 10 miles distant, although in the first case the scrim net catch in the upper 25 m. (total volume 57 cc.) was composed entirely of crustacea and in the second case the corresponding catch (total volume 112 cc.) contained 109 cc. of ceratium and only 3 cc. of crustacea. We may conclude therefore that the changes in transparency at our three stations were not due *directly* to the abundance of either the zooplankton or the phytoplankton. A similar conclusion was reached by Poole and Atkins ('29) and by Clarke ('38), but Williams and Utterback ('35) found "considerable correlation" with the total plankton.

An *indirect* relationship may exist, however, between the abundance of plankton and transparency in that the animals and plants may affect the rate of light absorption after they have died and disintegrated. The decomposing plankton material may accumulate in clouds and exert an obscuring effect, it may sink to the bottom and add to the detritus later to be stirred up, or it may influence light absorption after it has gone into solution. Probably the finest particles have the greatest effect on the transparency of the sea. Clarke and James ('39) found that the transmission of samples of sea water was greatly increased by filtering through a Berkefeld candle. Furthermore, even after Berkefeld filtering, samples of coastal water exhibited a highly selective action on light (beyond that of pure water itself). Thus coastal water was shown to contain material of filter-passing dimensions which exerted an important influence on transparency. Accordingly, an area of the ocean with an abundant and variable plankton would be expected to fluctuate in respect to transparency although no exact correlation be found with the catches of living plankton. Whether this indirect action of the plankton has a greater or a lesser effect on transparency than the periodic admixture of mud from the bottom and the shore remains to be determined. There is no doubt that the progressively reduced influence of both these factors in the slope water and the Sargasso water accounts for their greater clearness.

The effect which the foregoing variations in *rate* of absorption will have on the intensity of the submarine illumination is very different depending upon the depth of water considered as well as upon the magnitude of the extinction coefficient. An organism living at a depth of 50 m. in the slope water would have received a percentage of the surface light which was about 12 × greater when the water was the clearest than when it was the most turbid (Table III).

TABLE III. *Effect of variation in transparency on the illumination at two depths in the three areas*

Area		Percentage of surface light reaching designated depths *		
		Maximum Per cent	Minimum Per cent	Average Per cent
Coastal water	50 m.	0.41	0.06	0.15
Slope water	50 m.	8.2	0.67	2.9
Sargasso water	50 m.	12.2	3.7	7.8
Slope water	500 m.	2×10^{-9}	2×10^{-20}	4×10^{-14}
Sargasso water	500 m.	8×10^{-8}	3×10^{-13}	8×10^{-10}

* Disregarding "surface loss."

In the coastal water, at the same depth, the difference produced by the variations observed in the transparency would make a 7-fold change in the illumination, whereas in the Sargasso Sea the light at 50 m. would be only a little more than 3 × as bright on one occasion as on another.[7] At a depth of 500 m., however, in the Sargasso Sea the proportion of daylight present would be more than 100,000 × greater when absorption was at a minimum than when it was at a maximum (if we assume that the water below the greatest depth of actual measurement had the same transparency as that above). In the slope water a difference as great as $10^{11} \times$ would be encountered at 500 m. (see also Waterman, Nunnemacher, Chace, and Clarke, '39). It is therefore apparent that even slight differences in the transparency of oceanic waters produce great changes in the illumination beneath the surface and these must be of tremendous importance to photosensitive plants and animals.

---

[7] Disregarding seasonal changes in the intensity of daylight (Clarke, '38).

SUMMARY

1. Measurements were made throughout the year 1937–38 of the penetration of daylight into the sea at single stations located in the coastal area, the slope water area, and the Sargasso Sea between Long Island, N. Y., and Bermuda using Weston photronic cells with and without green filters.

2. The water was found to be optically homogeneous over the range of depth investigated in almost all cases and no significant difference existed below 2 m. in the rates of absorption of the total visible spectrum and of the green component of daylight.

3. The coastal water was the least transparent on all occasions (average absorption 12 per cent per meter), the Sargasso water was the clearest (absorption 5.1 per cent) and the slope water was intermediate (absorption 7.1 per cent).

4. Variation in transparency was greatest in the slope water area and is accounted for by the fluctuations in the amounts of Sargasso water and coastal water present. The variations in the other areas are not correlated directly with the plankton but may be, indirectly, through its disintegration products.

5. Very large changes in the illumination reaching the deeper strata, which must be important biologically, are produced by even slight variations in transparency.

LITERATURE CITED

Atkins, W. R. G., Clarke, G. L., Pettersson, H., Poole, H. H., Utterback, C. L., and Angstrom, A. 1938. Measurements of submarine daylight. *Jour. Conseil Perm. Intern. Exp. Mer.* **13**: 37–57.

Bigelow, H. B., and Sears, M. 1939. Studies of the waters of the continental shelf, Cape Cod to Chesapeake Bay. III. A volumetric study of the zooplankton. *Mem. Mus. Comp. Zool. at Harvard College* **54** (4): 183–377.

Clarke, G. L. 1936. Light penetration in the western North Atlantic and its application to biological problems. *Rapp. Procès—Verbaux. Con. Perm. Intern. Exp. Mer.* **101** (Pt. 2): 3–14.

——. 1938. Seasonal changes in the intensity of submarine illumination off Woods Hole. *Ecology* **19**: 89–106.

——. 1939. The utilization of solar energy by aquatic organisms. *Occasional Publications of A. A. A. S.* (In Press).

Clarke, G. L., and James, H. R. 1939. Laboratory analysis of the selective absorption of light by sea water. *Jour. Opt. Soc. Am.* **29**: 43–55.

Iselin, C. O'D. 1936. A study of the circulation of the western North Atlantic. *Papers Phys. Oceanography and Meteorology (Mass. Int. Tech. and Woods Hole Ocean. Inst.)* **4** (4): 101.

Oster, R. H., and Clarke, G. L. 1935. The penetration of the red, green and violet components of daylight into Atlantic waters. *Jour. Opt. Soc. Am.* **25**: 84–91.

Pettersson, H. 1934. Scattering and extinction of light in sea-water. *Göteborgs Kungl. Vetenskaps- och vitterhets-samhälles Handl.* (Femte foljden. Ser. B) **4** (4): 3–16.

Poole, H. H., and Atkins, W. R. G. 1929. Photo-electric measurements of submarine illumination throughout the year. *Jour. Mar. Biol. Ass.* **16** (n. s.): 297–324.

Powell, W. M., and Clarke, G. L. 1936. The reflection and absorption of daylight at the surface of the ocean. *Jour. Opt. Soc. Am.* **26**: 111–120.

Waterman, T. H., Nunnemacher, R. F., Chace, F. A., and Clarke, G. L. 1939. Diurnal vertical migration of deep water plankton. *Biol. Bull.* **76**: 256–279.

Whitney, L. V. 1938. Microstratification of inland lakes. *Trans. Wis. Acad. Sci., Arts and Let.* **31**: 155–173.

——. 1939. The general law of diminution of light intensity and the per cent of diffuse light at different depths in lake water. (In Press.)

Williams, E. A., and Utterback, C. L. 1935. Seasonal changes in components of submarine daylight. *Jour. Opt. Soc. Am.* **25**: 384.

Contribution No. 238

DISTRIBUTION OF ORGANIC MATTER IN MARINE SEDIMENTS AND ITS AVAILABILITY TO FURTHER DECOMPOSITION*

By

D. Q. ANDERSON

It has been shown, in previous contributions (*1*) from this Institution, that the organic matter of the marine bottom has a characteristic chemical composition, similar in many respects to the humus of field and garden soils. This organic matter is not inert but can undergo slow but gradual oxidation, a process shown (*2*) to be largely biological in nature. In shallower bottoms and closer to land, the organic matter was found to be oxidized more readily than that of deep seas. The non-nitrogenous constituents decomposed more readily than the nitrogenous substances, with the result that the carbon-nitrogen ratio of the organic matter tended to become narrower.

In the following experiments, an attempt has been made to extend the above studies, especially with reference to deep sea formations.

The muds used in these experiments were collected on the Oceanographic boats *Atlantis* and *Asterias*, by the use of a modified Ekman mud sampler, 3 inches in diameter and twenty four inches long. The cores of mud varied from 10 to 23 inches in length. The brass section of the mud sampler above the core tube was weighted with molded lead and fitted with a one way valve which prevented water from flushing out the mud as it was being hauled to the surface. The tube containing the mud was disconnected from the rest of the sampler and the mud forced upwards by a modified wooden ramrod which was fastened to the deck. If desired the bottom water directly above the mud with the very light brownish ooze which is ordinarily lost with other types of samplers could be siphoned into a jar and saved for chemical analysis and for oxidation studies. Ordinarily the mud was taken from the core tube in an undisturbed condition. The thin layer of mobile brownish ooze which was sometimes almost slimy was saved together with the highly viscous surface mud and included with the top section; the latter varied from one half to one inch in thickness.

The ramrod was fitted with a collar which could be lowered as desired thus preventing the mud from slipping out of the core tube. This permitted inspection of 3 to 4 inch layers of the mud while being removed. These sections were kept in clean glass jars until used. The sections which appeared to be high in organic matter or with an excess water were stored on ice.

---

* Contribution No. 238 of the Woods Hole Oceanographic Institution.

Reprint from SEARS FOUND. JOURN. MAR. RES.

When brought to the laboratory, the mud was carefully mixed and representative portions suspended in definite volumes of aged sea water. Considerable shaking and stirring with a glass rod was required to suspend the mud. It is believed that this treatment satisfied at least for the moment the chemical affinity which certain marine muds are known to have for oxygen. Among the factors causing this phenomenon are extremely low oxidation reduction potentials, large amounts of hydrogen sulphide, as well as reduced or partly reduced iron present in the mud.

The sea water was collected at considerable distances from land in order to avoid terrestrial contamination. After filtering through several layers of fine silk cloth, the water was stored for at least a month in the dark, then aerated several times, and, after the oxygen reached an equilibrium, used as dilution water.

Aliquot portions of diluted mud were added to several 225 ml. oxygen bottles, as well as to dried filter paper; the latter were dried at 105° C. to ascertain the weight and moisture contents of the sample used. The oxygen bottles were carefully filled with aged sea water. Some of the bottles were analyzed for oxygen after 1 to 2 hours; others were incubated in a water bath in the dark for 5, 10 and 15 days; they were shaken daily for the first 5 days and then every other day. When ready for analysis, the supernatant liquid was siphoned into smaller 125 ml. oxygen bottles and Winkler reagents added. Only the 15 day results are reported in the Tables.

The organic carbon content of the mud was determined by a modification of the Schollenberger method (*1*). Since marine muds, especially the surface of the cores, contain considerable amounts of sea-water, silver sulphate was added to arrest decomposition of the NaCl by the chromic acid. All samples were analyzed in duplicate with and without the addition of silver sulphate. With this modified method, the carbon equivalents of the respective mud were found to be lower by a fraction of a milligram to a few milligrams except in those cases where the moisture content of the mud was very low; the carbon content was then about the same with and without the addition of silver sulphate. Nitrogen was estimated by the Kjeldahl method using potassium persulphate as a catalyst.

The muds used in this study came from 35 to 43 degress North Latitude and from 67 to 70 degrees West Longitude, varying in depth from a few meters to over 5,100 meters. The muds from the higher latitudes were covered with water of arctic origin, whereas the southern muds were covered with highly saline tropical water. Whenever possible, muds were collected in an undisturbed state, and divided into at least 3 sections: top, intermediate and bottom. The respective layers varied from one half to four inches in length. At other times cores were divided into their natural stratified layers. The availability of the organic matter in the mud was calculated on the basis of oxygen consumed per 1 gram of organic carbon in the mud.

Table I gives the results of top sections of cores collected at various distances from land. The sand, water sample and surface material of mud 158 were collected in Dr. Stetson's sand pans. The pans were weighted down so that they could not be easily moved and were fitted with a mechanical device that blocks off the opening into the pan as they are being hauled to the surface. A rope was attached to the pan and to a buoy so it could be found after being allowed to collect sand and silt for a day or so. The yield of sand in any one of these pans was rather small, so that a composite was made of the water and sand in several of these pans. The top water contained considerable amounts of light flocculent materials. This water was siphoned into oxygen bottles and oxygen determinations made after 5, 10, 15 and 34 days. It was found that 1.39 cc. of oxygen was consumed during the first 5 days, increasing to 1.66 cc. in 10 days and to 2.24 cc. per liter in 15 days; the latter figure held after 34 days. The supernatant liquid contained considerable flocculent material, in addition to a certain amount of fine sand; 195 cc. of oxygen were consumed per 1 gram of carbon in this material, while the sand consumed 260 cc. of oxygen per 1 gram of carbon present.

The organic carbon varied from 4.5 per cent in muds collected from Hadley Harbor, Naushon Island, to 0.5 per cent at considerable distance from land. The availability of the organic matter to bacterial decomposition is reported as cc. of oxygen utilized per 1 gram of carbon present in the mud. The oxygen consumption in 15 days varied from 260 cc., in sand collected near shore, to 23 cc. in mud collected at considerable distance from land. The availability of the organic matter in mud 9 containing 4.5 per cent organic carbon was only slightly greater than that of mud 135, which contained only 0.86 per cent carbon. Generally, however, the carbon became less available at greater depths and greater distances from land.

Table I indicates the type of record kept on muds collected off Nomans land. All sections of the respective cores were examined. For lack of space, certain intermediate sections of mud were not reported. These muds showed no significant differences from the layer above or below and served only as additional analysis or to indicate the trend, as determined by biological oxidation and by carbon and nitrogen content.

The first five muds were collected in the immediate vicinity of Woods Hole. Muds 42 to 78 are from Massachusetts Bay, in a line almost parallel to 43° North Latitude going east off the coast of Massachusetts and New Hampshire past the Isle of Shoals to a point about twenty five miles from land. Muds 91 to 111 are a line of stations going east from the northern part of Cape Cod Massachusetts. Muds 112 to 156 were collected along a line from Block Island, Rhode Island to within a hundred and fifty miles from Bermuda.

In order to obtain information on the effect of different types of organic matter on bacterial decomposition, different sections of the same core were added to oxygen bottles and oxidation studies made. The rate and amount of oxygen consumed can be used as a measure of the availability of the organic matter in the mud. In considering the extent to which the organic matter was attacked by microorganisms only the 15 day period is reported.

One would ordinarily expect that the organic matter in the surface layer of the core would be most easily decomposed, the rate of decomposition gradually decreasing downwards. This was true in about half of the cores examined. In certain cases, as in samples 22, 24 and 25, the top and middle layers were equally available, oxygen consumption being 79 and 82 cc. respectively, whereas the intermediate layer consumed 107 cc. oxygen. In core 42, 44 and 45, the top was least resistant to oxidation, the intermediate most resistant, whereas the organic matter in the bottom layer was somewhat more available than the middle section.

In samples 62 to 66, it was necessary to remove the fine gravel before the mud could be suspended in water. In the top section 1000 cc. of oxygen were utilized per one gram of carbon. This is more than half the theoretical required for complete oxidation of all of the organic matter. This was nearly four times as great as the consumption of oxygen by the mud directly under it and about ten times that of most samples. It is quite probable that this sample of mud contained some fresh animal or fresh plant material.

In muds 91 to 95 the moisture was exceptionally low and the respective layers appeared to be rather homogeneous i. e., without evidence of stratification. The carbon content was rather uniform throughout the entire 15 inches, while the nitrogen decreased from 0.078 to 0.056 per cent in the bottom sample. The maximum oxygen consumption, 198 cc. per gram of organic carbon, occurred in the intermediate layer, it decreased to 86 cc. in the surface and 127 cc. in the bottom. Here again the organic matter which had been buried for some time under anaerobic conditions was two and one half times more easily decomposed than the carbon in the surface mud, while the organic complex in the bottom material was more available than the surface material but only 60 per cent as easily decomposed as the intermediate layer.

Samples 112, 114 and 118 were conspicuous because of the absence of decomposable organic matter below the 5 inch layer. The organic carbon in the top inch was twice as available as that in the next layer. The nitrogen content was uniform namely, 0.03 to 0.04 per cent throughout the core.

Samples 120, 126 and 127, one hundred ninety five miles from land and 2873 meters deep, were decidedly different from the muds 112–118, in that they contained considerable decomposable organic matter. The surface ooze consumed the greatest amount of oxygen.

Samples 142, 145 and 148 were 100 miles from land and 384 meters deep. The oxygen consumed increased from 23 cc. in the top material to 49 in the

8 to 12 inch section and to 105 cc. in the 19 to 23 inch layer. The 15 to 19 inch portion was a whitish clay, whereas the mud, both above and below this layer was sandy, that of the top being coarser than the bottom.

Mud 150 to 156 was in sight of Block Island and 67 meters deep. The top 1 inch layer consumed 55 cc., the 8–12 inch 102 cc. and the 12–16 inch 44 cc., increasing to 113 cc. at the bottom of the core.

Some idea may be gained concerning the nature of the different types of organic matter, if the amounts of oxygen consumed after 15 days are examined. The degree of oxidation depends on the availability of the organic matter. The spread of oxygen consumption is very great varying from zero to 1000 cc. per one gram of carbon present in the bottom sediment. If all the 131 samples tested are put in classes depending on their organic carbon content, it will be found (Figure 67) that there are two distinct groups of sediments. Twenty-five per cent of the muds contained between 0.67 and 0.99 per cent carbon, and 50 per cent contained 0.34 to 1.32 per cent carbon. The other large class of sediments contained 1.99 to 2.31 per cent of carbon, 26 per cent of the samples were within this range, whereas 38 per cent contained between 1.66 and 2.64 per cent carbon.

Similarly if the muds are classified according to the amount of oxygen consumed, it will be seen (Figure 67) that 29 per cent of the sediments utilized between 74 and 93 cc. of oxygen and 76 per cent utilized between 37 and 130 cc.

Since these curves are almost the antithesis of each other, it is apparent that there is no correlation between the amount of oxygen consumed and the amount of organic carbon present in the sediment, except when the carbon is low, namely below 0.3 per cent, when little or no oxygen will be utilized. According to theoretical calculations one gram of organic carbon will utilize 1,860 cc. of oxygen for complete oxidation to carbon dioxide. The oxygen consumption and carbon utilization have been calculated in terms of each other. If the oxygen consumption curve is interpolated in terms of per cent carbon utilization in the respective sediments, it is found that in the case of 29 per cent of the sediments, between 4 and 5 per cent of the carbon was oxidized and in case of 76 per cent 2 to 7 per cent of organic carbon was thus available.

Some idea of the rate of this oxidation may be gained if the oxygen utilization figures are averaged after 5, 10 and 15 days on the 131 samples on which complete oxidation studies were made. In 5 days, an average of 59 cc. of oxygen were utilized in 10 days 83 cc. and in 15 days 112 cc. corresponding to 3.2 per cent of the carbon in 5 days, 4.5 per cent in 10 days and 6.1 in 15 days.

Many of the muds reported in this investigation were analyzed by Waksman and Hotchkiss (*2*) in 1937. They reported the oxygen consumption per 1 gram of dry mud. These data have been recalculated to ascertain the

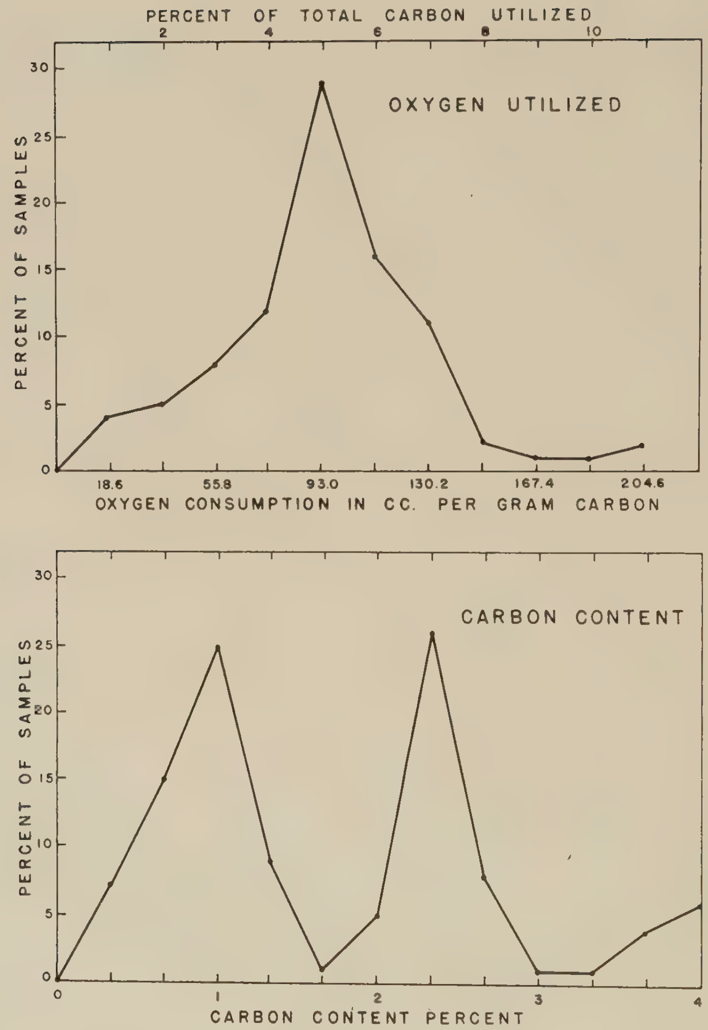


Figure 67. Oxygen consumption, carbon utilization and carbon content of marine mud.

amount of oxygen utilized per 1 gram of carbon present in the mud, compared with the muds collected from the same locality in this present investigation (1938), and reported in Table II. Since only the nitrogen content was reported for the 1937 data, the carbon content was calculated by using the factor 10 : 1. From an inspection of the data in Table I of this report and from previous reports by Waksman and co-workers the ratio of carbon to nitrogen in most marine bottoms is between 8 : 1 and 12 : 1, a large majority of these being 10 : 1. Muds collected in 1937 and 1938, in a line of stations off the Isle of Shoals, in Massachusetts Bay, and off Cape Cod are compared in chemical composition and availability of the organic matter after 15 days oxidation. The location of these stations and nitrogen content are given in Table 9,[1] Vol. 1, page 114, Journal Marine Research, and are referred to here as station number. In case of Station 1, there was, in 1937, a decrease in oxygen absorption from top to bottom from 80 to 68 cc.; in 1938 (2 cores), there was a similar decrease from top to bottom from about 200 cc. to 92 cc. The nitrogen content of the two samples of 1937 mud was 0.193 and 0.139 per cent, whereas the nitrogen content of the samples taken in 1938 was only about half as large, decreasing from 0.090 and 0.114 at the surface to 0.072 and 0.024 in the bottom of the core.

In Station 2, the oxygen absorbed per 1 gram of carbon increased from top to bottom of the core, namely from 74 cc. to 86 cc. in 1937 and from 166 cc. to 238 cc. in 1938. Here again the surface material contained twice as much nitrogen in the 1937 samples than in the 1938 samples, whereas the bottom material contained about 18 per cent as much nitrogen as the sample collected in 1937.

The surface material in the mud from Station 3 collected in 1938 was very easily decomposed. One thousand cubic centimeters of oxygen were absorbed per 1 gram of carbon. The bottom material utilized 274 cc. of oxygen. In 1937 this mud utilized 70 cc. of oxygen in the surface material and increased to 96 cc. in the remainder of the core. Attention has already been called to the possible abnormality of the 1938 sample.

The mud from Station 4 (1937) increased in oxygen consumption from 47 cc. in the **A** layer to 105 cc. in the **B** layer; in 1938, the top layer utilized 137 cc., the intermediate 91 cc. and the bottom 36 cc. of oxygen. The nitrogen content of the surface material was almost the same during both years. namely 0.252 and 0.272 per cent, decreasing in 1937 in the **B** horizon to 0.192 and in 1938 to 0.136.

In Stations 6, 7 and 8, the organic matter collected in 1938 was more available than that collected in 1937, and was uniform throughout the entire core. Stations 9 to 12 were all from the same vicinity of a 99 fathom hole in Massachusetts Bay. In 1937, the nitrogen content of the top layer of the cores varied from 0.081 to 0.245 per cent. In other words, one sample of mud contained 3 times more than another sample a few meters away. Similarly the nitrogen content in the **B** layer varied from 0.051 to 0.228 per cent. The oxygen consumption per 1 gram of carbon present in the mud fluctuated from 8 to 106 cc. In 3 cases out of 4, the bottom material was more available than the top by about 2 times. In 1938, two cores were collected from this locality and analyzed. In general, there was a decrease in availability of the carbon from top to bottom. In one case, the middle layer was only half as available as either the top or bottom. One hundred seventy-nine cc. of oxygen were utilized in the top inch, 97 cc. in the 3–6 inch, and 224 cc. in the 10–15 inch section. In one sample the nitrogen decreased from 0.258 per cent in the top layer to 0.168 in the 9–15 inch layer; in another sample the decrease from top to bottom was from 0.126 to 0.040 per cent.

---

[1] Position reported W. Lat. N. Long. should have been N. Lat. W. Long.

In Station 14, collected off Cape Cod in 1937, 77 cc. of oxygen were utilized in the **A** layer and 153 cc. in the **B** layer. In 1938 there was a similar increase in the availability of the organic carbon from top to bottom, namely 85 cc. in the surface material, 149 cc. in the 7–10 inch layer, and 127 cc. in the 10–15 inch layer. Fifty-four and 55 cc. of oxygen were utilized per 1 gram of carbon in the top and bottom layers of mud from Station 15 in 1937. In 1938, the oxygen consumption was somewhat higher but about the same range, namely 85 cc. in the top and 82 cc. in the 12–15 inch layer. In 1937, the nitrogen content was about the same throughout the core, whereas in 1938 the nitrogen decreased from 0.239 in the top to 0.183 per cent in the bottom layer.

In the mud collected from Station 16, there was an increase in oxygen absorption in the bottom material over the top, both years, namely from 47 cc. to 62 cc. in 1937, and from 64 cc. and 111 cc. in 1938. Here again, the nitrogen was uniform from top to bottom in the 1937 core, whereas, in the 1938, it decreased from 0.182 to 0.157 per cent from top to bottom. In 1938, more oxygen was absorbed per 1 gram of carbon present in the mud from Station 17 than in 1937. The 1938 sample showed a decrease from 111 cc. to 91 cc. in 16 inches, whereas in 1937 the oxidation of the mud increased from 45 cc. to 60 cc. oxygen in the **A** and **B** layer.

The amount of oxygen absorbed per 1 gram of carbon in 14 or 15 days was generally higher in 1938 than in 1937. In certain cases they compare favorably; in other cases the bottom mud was more available than the top one year, whereas the next year the top material was more available than the bottom. No explanation could be offered at present for these differences. Presumably, the experimental procedures were about the same both years. In 1937, the muds were collected in a glass tube about 15 mm. in diameter and the amount of material available for the respective experiments and for chemical analyses, particularly of the top material, was limited. In 1938, however, the muds were collected in a three inch core tube, ten to twenty times more material being thus collected, and should, therefore, be more representative. One may speculate further as to whether a small tube causes the light mobile surface material of the core to be pushed away from the cutting edge of the tube more easily than in the case of the larger tube.

More information is needed concerning the sedimentation of the bottom material and its chemical nature, before the significance of the oxidation of the organic matter can be interpreted.

The author is indebted to Dr. Bigelow and Dr. Renn for permission to use instrument for taking bottom cores and for assistance generously rendered in numerous ways, and to Dr. Waksman, for outlining the problem.

REFERENCES

(*1*) Waksman, S. A.

1933. On the distribution of organic matter in the sea bottom and the chemical nature and origin of marine humus. Soil Sci *36:* 125–147.

(*2*) Waksman, S. A., Hotchkiss, M.

1938. On the oxidation of organic matter in marine sediments by bacteria. Jour. Mar. Res. *1:* 101–118.

TABLE I

Chemical and Biological Analysis of Marine Muds

Sample number	*Location*	*Depth, meters*	*Distance from land, miles*	*Layer, inches*	*Moisture, %*	*Carbon, %*	*Nitrogen, %*	*Ratio C/N*	*Oxygen consumed, cc. per 1 gm. carbon in 15 days*
9	Hadley Harbor	6	.02	0–2	72	4.50	.318	14.1	51
11	Hadley Harbor	6	.02	0–1	73	4.32	.350	12.2	66
13	Hadley Harbor			3–8	62	3.33	.252	13.3	47
22	Buzzards Bay	15	2.0	0–½	64	2.35	.220	10.6	79
24	Buzzards Bay			2–4	52	2.10	.195	10.8	107
25	Buzzards Bay			4–6	51	2.46	.197	12.5	82
1	Buzzards Bay	15	1.0	0–½	—	2.11	.220	9.6	82
27	Buzzards Bay	15	2.0	0–8	59	2.16	.262	8.2	62
158	Buzzards Bay	5	.1	water	100	—	—	—	2.2**
158	Buzzards Bay	5	.1	*	92	.73	.076	9.6	195
158	Buzzards Bay	5	.1	sand	15	.11	.020	5.6	260
42	42° 57′ N., 70° 31′ W.	83	11.7	0–2	62	.99	.114	8.7	219

* Supernatant liquid plus ooze.

** Oxygen consumed cc. per liter.

TABLE I continued on next page.

TABLE I—*Continued*

CHEMICAL AND BIOLOGICAL ANALYSIS OF MARINE MUDS

Sample number	*Lccation*	*Depth, meters*	*Distance from land, miles*	*Layer, inches*	*Moisture, %*	*Carbon, %*	*Nitrogen, %*	*Ratio C/N*	*Oxygen consumed, cc. per 1 gm. carbon in 15 days*
44	42° 57′ N., 70° 31′ W.			5–9	42	.35	.024	14.1	92
45	42° 57′ N., 70° 31′ W.			9–14	44	.46	.032	14.3	128
39	42° 57′ N., 70° 31′ W.	83	11.7	0–1½	60	.84	.090	9.3	195
52	42° 57′ N., 70° 27′ W.	100	14.8	0–1	54	.91	.100	9.1	166
62	42° 57′ N., 70° 25′ W.	100	16.2	0–1	65	.46	.062	7.4	1000
65	42° 57′ N., 70° 25′ W.			13–16	40	.30	.024	12.5	266
67	42° 57′ N., 70° 22′ W.	140	18.3	0–1½	72	2.26	.272	8.3	137
71	42° 57′ N., 70° 20′ W.	159	20.0	0–1	73	2.26	.272	8.3	130
76	42° 57′ N., 70° 18′ W.	164	21.5	0–1	71	2.31	.246	9.4	103
77	42° 57′ N., 70° 18′ W.			1–3	57	2.23	.212	10.5	143
78	42° 57′ N., 70° 18′ W.			9–12	57	2.20	.242	9.9	117
81	42° 59′ N., 70° 15′ W.	155	22.7	0–1	74	2.30	.271	8.5	112
86	42° 59′ N., 70° 12′ W.	175	24.9	0–1	68	2.35	.252	9.3	90
29	42° 30′ N., 70° 18′ W.	168	16.5	0–½	71	2.34	.258	9.1	95
34	42° 30′ N., 70° 18′ W.	160	16.5	0–1	68	1.16	.126	9.2	197
36	42° 30′ N., 70° 18′ W.			3–6	34	.67	.062	10.8	97
38	42° 30′ N., 70° 18′ W.			10–15	42	.48	.040	12.0	214
91	42° 00′ N., 69° 46′ W.	150	12.9	0–½	42	.60	.078	7.7	85
93	42° 00′ N., 69° 46′ W.			3–7	34	.57	.052	10.9	198
95	42° 00′ N., 69° 46′ W.			10–15	30	.66	.056	10.8	127
97	42° 01′ N., 69° 43′ W.	165	14.3	0–1	73	2.06	.232	8.9	111
107	42° 01′ N., 69° 38′ W.	210	17.9	0–1	68	1.78	.182	9.8	64
111	42° 01′ N., 69° 38′ W.			13–16	57	1.77	.157	11.3	111
102	41° 59′ N., 69° 41′ W.	168	13.6	0–½	73	2.02	.239	8.9	85
106	41° 59′ N., 69° 41′ W.			12–15	58	2.19	.183	11.9	82
157	40° 37′ N., 71° 38′ W.	67	30	*	92	.94	.144	6.5	110
150	40° 37′ N., 71° 38′ W.			0–1	62	1.14	.116	9.8	55
153	40° 37′ N., 71° 38′ W.			8–12	38	.56	.092	6.1	102
154	40° 37′ N., 71° 38′ W.			12–16	42	.10	.090	11.4	44
156	40° 37′ N., 71° 38′ W.			19–22½	34	.10	.076	13.2	113
149	40° 13′ N., 71° 27′ W.	85	55	0–8	51	.49	.046	10.7	119
142	39° 57′ N., 71° 11′ W.	384	100	0–1	70	1.30	.142	9.2	23
145	39° 57′ N., 71° 11′ W.			8–12	37	.87	.082	10.6	49
148	39° 57′ N., 71° 11′ W.			19–23	38	.80	.072	11.1	105
140	39° 39′ N., 70° 53′ W.	2285	120	0–½	54	.86	.106	8.1	40
128	39° 17′ N., 70° 28′ W.	2800	150	0–½	65	.94	.058	16.2	23
127	39° 00′ N., 70° 16′ W.	2873	195	*	89	.85	.054	15.8	132
120	39° 00′ N., 70° 16′ W.			0–1	69	.73	.083	8.8	23
126	39° 00′ N., 70° 16′ W.			16–19	53	.86	.072	11.9	80
119	35° 05′ N., 67° 05′ W.	5233	450	*	89	.86	.066	13.0	23
112	35° 05′ N., 67° 05′ W.			0–1	49	.57	.036	15.8	51
114	35° 05′ N., 67° 05′ W.			5–8	46	.33	.030	11.0	0
118	35° 05′ N., 67° 05′ W.			17–20	47	.24	.038	6.3	0

TABLE II

Comparison of Oxygen Consumption and Chemical Composition of Bottom Materials from a Line of Stations off Massachusetts Bay, Isle of Shoals and Cape Cod, Collected in 1937 and in 1938

Station No.	*Layer*	*1937*		*1938*			
		Carbon % (calc.)	*Oxygen consumed*[1] *cc.*	*Section inches*	*Nitrogen %*	*Carbon %*	*Oxygen consumed*[1] *cc.*
1	A	1.93	80	0–1½	.090	.84	195
				0–2	.114	.49	219
	B	1.39	68	5–8	.072	.68	94
				5–9	.024	.36	92
2	A	2.09	74	0–1	.100	.91	166
	B	1.73	86	9–12	.032	.44	238
3	A	1.38	70	0–1	.062	.46	1000
	B	.48	96	9–13	.018	.27	274
4	A	2.52	47	0–1½	.272	2.26	137
				4–8	.162	2.14	91
	B	1.92	105	8–14	.136	2.04	36
5	A	2.91	42	0–1	.272	2.26	130
				6–9	.218	2.38	91
	B	2.54	54	9–12	.224	2.35	115
6	A	3.06	33	0–1	.246	2.31	103
	B	2.72	46	9–12	.242	2.20	117
7	A	2.88	55	0–1	.227	2.30	112
	B	2.27	58	9–13	.210	2.17	107
8	A	3.26	57	0–1	.253	2.35	90
				8–12	.150	2.21	94
	B	.81	38	12–16	.168	2.17	108
9	A	.81	8				
10	A	1.79	49	0–½	.258	2.34	95
				2½–5	.172	1.99	81
	B	.51	92	9½–15	.168	1.98	82
11	A	1.62	51	0–1	.126	1.16	197
				1–3	.124	1.00	81
	B	1.76	106	3–6	.062	.67	97
				6–10	.042	.63	112
12	A	2.45	54	10–15	.040	.48	204
	B	2.11	69				
14	A	.81	77	0–½	.078	.60	85
				7–10	.050	.69	149
	B	.47	153	10–15	.056	.66	127
15	A	2.60	54	0–½	.239	2.02	85
	B	2.61	55	15–15	.183	2.19	82
16	A	2.33	47	0–1	.182	1.78	64
	B	2.34	62	13–16	.157	1.77	111
17	A	2.26	46	0–1	.232	2.06	111
	B	2.04	60	12–16	.182	1.85	91

[1] Per 1 gram of carbon present in mud, in 14 days in 1937, and in 15 days in 1938.

Contribution No. 243

RESULTADOS DE LA PRIMERA EXPEDICION EN LAS ANTILLAS DEL KETCH ATLANTIS BAJO LOS AUSPICIOS DE LAS UNIVERSIDADES DE HARVARD Y HABANA

Nuevo Género y Especies Nuevas de Foraminíferos

POR PEDRO J. BERMÚDEZ
Museo Poey, Universidad de la Habana.

Las especies nuevas que se describen a continuación proceden de la primera expedición a bordo del Atlantis.

Famalia *Ellipsoidinidae*

Género **Ellipsoglandulina** Silvestri, 1900.

Ellipsoglandulina antillea Bermúdez n. sp.

(Lám. 33, figs. 1-2)

Concha oval, con el extremo apertural más aguzado que el apical; una cámara hace la casi totalidad de la concha, en el extremo apical se notan restos de las primeras cámaras, pero sin suturas visibles; periferia circular; pared calcárea, lisa y pulida, de consistencia compacta, de color blanco lechoso, con finas perforaciones; abertura terminal en forma de hendidura alargada y algo comprimida en los bordes.

Largo 1 mm.

El holotipo en la colección Cushman, Sharon, Mass. U. S. A., procedente de Atlantis Sta. 2971 (Lat. 20° 34′ N. Long. 74° 24′ W.) 810 brazas de profundidad. Rara.

Contribution No. 243 of the
Woods Hole Oceangraphic Institutio

Esta especie es comparable con *Ellipsoglandulina labiata* (Schwager),(1) procedente del Terciario, de la que difiere por su forma más alargada y por que la concha de nuestra nueva especie está formada por la última cámara casi exclusivamente, mientras que la de Schwager deja ver varias cámaras en la primera porción.

Familia *Miliolidae*

Género **Riveroina** Bermúdez n. gen.

Genoholotipo *Riveroina caribaea* Bermúdez n. sp.

Concha libre, calcárea, aporcelanada, imperforada, planispiral, cámaras numerosas, alargadas, encorvadas y provistas de tabiques que forman multitud de camaritas. Las cámaras del *juvenarium* parecen *quinqueloculina,* lo que es difícil de ver por el engrosamiento de la pared de esta región.

Exteriormente se parece al género *Spiroloculina,* del que difiere por carecer de diente en la abertura y por los tabiques suplementarios que dividen las cámaras en muchas camaritas.

Este género nuevo ha sido nombrado en honor del Dr. Luis Howell Rivero, Profesor de Zoología en la Universidad de la Habana.

Riveroina caribaea Bermúdez n. sp.

(Lám. 33, figs. 3-4, text fig. 1)

Concha libre; pequeña, algo más larga que ancha, aguzándose en ambos extremos; pared calcárea, aporcelanada, mate y con exceso de material en la pared de la primera porción; planispiral; cámaras numerosas, seis u ocho forman la totalidad de la concha, proyectándose en ambos extremos, las dos últimas son las más prominentes y constituyen una gran parte de la concha; suturas salientes, las dos últimas forman dos gruesos rebordes que son visibles por ambos lados de la concha, el borde de la concha es anchamente redondeado y ligeramente ondulado; cámaras alargadas y encorvadas, divididas por tabiques internos en muchas camaritas, llegando hasta tener doce en las últimas, estas divisiones se notan al exterior como depresiones suaves; abertura en la proyección de la última cámara, simple, colocada como una hendidura transversalmente al eje de la concha.

---

(1) Schwager, 1866, Novara Expedition, Geol. Theil, pt. 2, p. 237, pl. 6, fig. 77.

Largo 0.7 mm., ancho 0.5 mm.

Holotipo en la colección Cushman, Sharon, Mass. U. S. A., procedente de Atlantis Sta. 2995 (Lat. 23° 24′ N. Long. 81° 00′ 30″ W.) 605 brazas de profundidad. Frecuente. Además se ha encontrado rara en las siguientes estaciones:

ATLANTIS STAS.
Sta. 2963.
Lat. 22° 12′ N. Long. 81° 10′ W. 190 brazas de profundidad.

Sta. 2980.
Lat. 22° 47′ N. Long. 78° 40′ W. 250 brazas de profundidad.

Esta interesante especie pasa desapercibida por su pequeño tamaño. Su aspecto, a primera vista, es como el de cualquier *Spiroloculina,* pero secciones en el plano de crecimiento de la concha han revelado una curiosa estructura interna, desconocida en la familia *Miliolidae;* estas divisiones de las cámaras no se han observado en ningún género del grupo de los que yo tengo conocimiento.

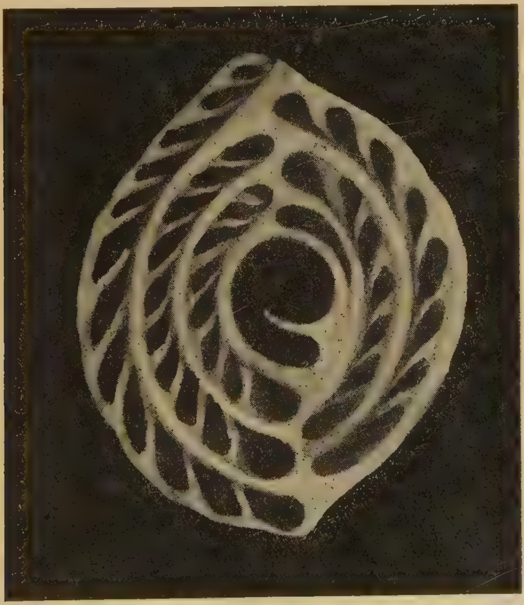


FIG. 1. *Riveroina caribaea* Bermúdez.
Sección horizontal. X ± 90

Familia *Buliminidae*

Género **Reussella**

Reussella aguayoi Bermúdez n. sp.

(Lám. 33, fig. 5)

Concha triangular, con los tres lados ligeramente cóncavos; extremo inicial agudo, truncada en el extremo apertural; cámaras numerosas, seis u ocho visibles en la superficie externa que van gradualmente aumentando de tamaño; con tres quillas cortantes y terminadas en espinas prominentes, que corresponden al final de las suturas de las cámaras que son ligeramente limbadas; pared gruesa, calcárea, con lustre vítreo y con muy finas perforaciones; abertura simple, en forma de coma, en la cara septal de la última cámara.

Largo 0.9 mm.

Holotipo en la colección Cushman, Sharon, Mass., U. S. A., procedente de Atlantis Sta. 2977 (Lat. 21° 42' N. Long. 76° 59' W.) 1175 brazas de profundidad. Rara.

Se distingue fácilmente de *Reussella spinulosa* (Reuss), por su forma más corta, y por sus espinas más prominentes.

Nombrada en honor del Dr. Carlos G. Aguayo, Profesor de Zoología de la Universidad de la Habana.

Anomalina atlantis Bermúdez n. sp.

(Lám. 33, figs. 6-8)

Concha libre; nautiloide, envuelta; contorno periférico ligeramente lobulado, sin quilla; plana o ligeramente cóncava por el lado ventral, convexa por el lado dorsal y con una ligera depresión hacia el centro; una vuelta y media de la espira visible por el lado ventral, y una sola vuelta visible por el lado dorsal, ocho cámaras en la última vuelta de la espira; pared espesa, con perforaciones gruesas en toda la superficie de la concha; abertura en la base de la última cámara pasando a ambos lados de la concha, siguiendo por el borde de las cámaras anteriores pareciendo una cortadura a lo largo de la base de las cámaras.

Diámetro 0.9-1 mm.

Holotipo en la colección Cushman, Sharon, Mass., U. S. A., procedente de Atlantis Sta. 2963 (Lat. 22° 12' N. Long. 81° 10' W.) 190 brazas de profundidad. Frecuente.

Esta nueva especie tiene mucho parecido con *Anomalina grosserugosa* H. B. Brady (no Gümbel) que aparece ilustrada en el Reporte del Challenger, pl. 94, figs. 4 a-c., y fué considerada por Thalmann como una nueva especie en su Nomenclator. La especie ilustrada por Brady (fig. 4) procede de la Sta. 344. Ascension Island, Océano Atlántico, 420 brazas de profundidad.

EXPLICACION DE LA LAMINA 33

Figs. 1-2. *Ellipsoglandulina antillea* Bermúdez n. sp. X.

Fig. 1, Holotipo visto de frente; fig. 2, Cotipo visto de lado. Atlantis Sta. 2971 (Lat. 20° 34′ N. Long. 74° 24′ W.) 810 brazas de profundidad.

„ 3-4. *Riveroina carabaea* Bermúdez n. gen. & n. sp. X.

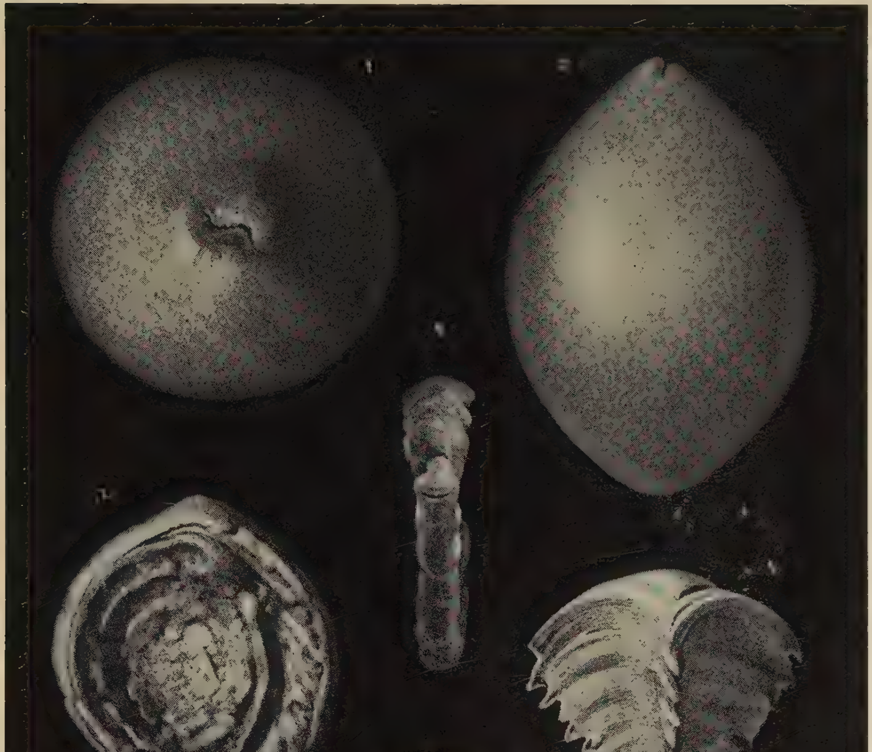
Fig. 3, Holotipo visto de lado; fig. 4, Cotipo visto de frente. Atlantis Sta. 2995 (Lat. 23° 24′ N. Long. 81° 00′ 30″ W.) 605 brazas de profundidad.

„ 5. *Reussella aguayoi* Bermúdez n. sp. X.

Holotipo visto de lado. Atlantis Sta. 2977 (Lat. 21° 42′ N. Long. 76″ 59′ W.) 1175 brazas de profundidad.

„ 6-8. *Anomalina atlantis* Bermúdez n. sp. X.

Fig. 6, Cotipo visto de frente; fig. 7; Holotipo vista ventral; fig. 8; Cotipo vista dorsal. Atlantis Sta. 2963 (Lat. 22° 12′ N. Long. 81° 10′ W.) 190 brazas de profundidad.



Report of the year 1938

THE
WOODS HOLE OCEANOGRAPHIC INSTITUTION

REPORT FOR THE YEAR
1938

TABLE OF CONTENTS

Page

I Trustees, as of December 31, 1938 3

II Members of the Corporation, as of December 31, 1938 ... 4

III Report of the Treasurer 5

IV Report of the Director 9

V Staff, as of December 31, 1938 20

APPENDIX: Reports of progress by investigators working at the Institution during 1938 21

I. TRUSTEES

(As of December 31, 1938)

To serve until 1942

Charles Francis Adams, Boston, Mass.
Thomas Barbour, Museum of Comparative Zoölogy, Cambridge, Mass.
John A. Fleming, Carnegie Institution, Washington, D.C.
Frank B. Jewett, New York, N.Y.
Albert Eide Parr, Bingham Oceanographic Foundation, New Haven, Conn.
Elihu Root, Jr., New York, N.Y.

To serve until 1941

The Commandant (Admiral R. R. Waesche), U. S. Coast Guard, for the time being, Washington, D.C.
Marion Eppley, Newport, R.I.
Lamar R. Leahy, U. S. Navy, Washington, D.C.
T. H. Morgan, California Institute of Technology, Pasadena, Calif.
The Director (Admiral L. O. Colbert), U. S. Coast & Geodetic Survey, for the time being, Washington, D.C.
B. W. St. Clair, Cambridge, Mass.

To serve until 1940

William Bowie, Washington, D.C.
A. G. Huntsman, University of Toronto, Toronto, Canada.
Columbus O'D. Iselin, Woods Hole Oceanographic Institution, Woods Hole, Mass.
Alfred C. Redfield, Harvard University, Cambridge, Mass.
Henry L. Shattuck, Boston, Mass.
T. Wayland Vaughan, Washington, D.C.

To serve until 1939

Isaiah Bowman, Johns Hopkins University, Baltimore, Md.
E. G. Conklin, Princeton University, Princeton, N.J.
Alexander Forbes, Harvard Medical School, Boston, Mass.
Ross G. Harrison, Yale University, New Haven, Conn.
Frank R. Lillie, University of Chicago, Chicago, Ill.
Harlow Shapley, Harvard University, Cambridge, Mass.

Ex Officio

Henry B. Bigelow, Museum of Comparative Zoölogy, Cambridge, Mass.
Lawrason Riggs, Jr., New York, N.Y.

OFFICERS

Frank R. Lillie, President of the Corporation, University of Chicago, Chicago, Ill.
Lawrason Riggs, Jr., Treasurer, 120 Broadway, New York, N.Y.
Henry B. Bigelow, Clerk of the Corporation, Museum of Comparative Zoölogy, Cambridge, Mass.

II. MEMBERS OF THE CORPORATION

(As of December 31, 1938)

Charles Francis Adams, Boston, Mass.
Thomas Barbour, Museum of Comparative Zoölogy, Cambridge, Mass.
Henry B. Bigelow, Museum of Comparative Zoölogy, Cambridge, Mass.
William Bowie, Washington, D.C.
Isaiah Bowman, Johns Hopkins University, Baltimore, Md.
The Commandant (Admiral R. R. Waesche), U. S. Coast Guard, for the time being, Washington, D.C.
E. G. Conklin, Princeton University, Princeton, N.J.
The Director (Admiral L. O. Colbert), U. S. Coast & Geodetic Survey, for the time being, Washington, D.C.
Benjamin M. Duggar, University of Wisconsin, Madison, Wis.
Marion Eppley, Newport, R.I.
John A. Fleming, Carnegie Institution, Washington, D.C.
Ross G. Harrison, Yale University, New Haven, Conn.
A. G. Huntsman, University of Toronto, Toronto, Canada.
Columbus O'D. Iselin, Woods Hole Oceanographic Institution, Woods Hole, Mass.
Frank B. Jewett, New York, N.Y.
Lamar R. Leahy, U. S. Navy, Washington, D.C.
Frank R. Lillie, University of Chicago, Chicago, Ill.
Alfred L. Loomis, Tuxedo Park, N.Y.
T. H. Morgan, California Institute of Technology, Pasadena, Calif.
Albert E. Parr, Bingham Oceanographic Foundation, New Haven, Conn.
Alfred C. Redfield, Harvard University, Cambridge, Mass.
Lawrason Riggs, Jr., New York, N.Y.
Elihu Root, Jr., New York, N.Y.
B. W. St. Clair, Cambridge, Mass.
Harlow Shapley, Harvard University, Cambridge, Mass.
Henry L. Shattuck, Boston, Mass.
T. Wayland Vaughan, Washington, D.C.

III. REPORT OF THE TREASURER

To The Members and Trustees of the
Woods Hole Oceanographic Institution:
Gentlemen:

The accounts for the year 1938 have been audited by Messrs. Stagg, Mather & Hough, public accountants.

During the year bonds costing $196,779.20 were sold or redeemed at a profit of $6,087.38, to which must be added $2,494.81 the reserve for amortization of bond premiums applicable to these bonds, making a total profit of $8,582.19. There was invested $177,486.75 from endowment cash in securities.

There was added to special income account, extra dividends on endowment fund stocks amounting to $1,487.50 and $306.75 dividends in stock and $436. income on the securities of the fund itself.

The gross income received during the year on the securities held at the end of the year in the endowment fund was .0420 of the cost of those securities, and .0435 of their then market value.

A grant of $1,000. was received from the Carnegie Corporation for operating expenses.

The operating expenses were under the budget by about $1,000. The expenses of upkeep of plant exceeded the budget by $5,746.68. Of this about $1,500. is due to repairs and improvement of the grounds after the hurricane (which considerably damaged the driveway and parking space) and the rest of the excess is due to the fact that replacements on the ship were made from current funds.

Summaries of the various accounts appear on pages 6, 7, and 8.

Respectfully submitted,
Lawrason Riggs, Jr.,
Treasurer

BALANCE SHEET

ENDOWMENT FUND ASSETS

	Quoted Market Value		
Endowment Fund assets:			
Bonds	$1,364,345.00	$1,438,299.51	
Stocks	$ 967,027.50	974,914.86	
Cash (including $553.25 due from current funds—Cash)		31,878.00	$2,445,092.37
Reserve fund assets:			
Bonds	$ 4,720.00	$ 5,470.00	
Stocks	$ 16,172.00	19,098.99	
Cash		2,275.65	26,844.64
			$2,471,937.01

PLANT ASSETS

Laboratory plant:		
Land	$ 27,072.32	
Buildings	323,213.12	
Laboratory equipment	21,361.93	
Crew room equipment	557.95	
Library	10,700.00	$ 382,905.32
Ship "Atlantis":		
Construction	$ 218,674.47	
Equipment	27,298.50	245,972.97
Small boat and equipment		6,570.55
		$ 635,448.84
Depreciation fund assets (for periodic replacements):		
Bonds (quoted market value $21,412.00)	$ 21,000.00	
Cash	12,648.02	33,648.02
		$ 669,096.86

CURRENT ASSETS

Current funds—Cash	$ 14,670.13	
Less—Due to Endowment fund cash	553.25	$ 14,116.88
Special income account:		
Investments:		
Bonds (quoted market value $12,780.00)	$ 12,375.00	
Stocks (quoted market value $ 1,946.25)	1,950.25	
Cash	6,020.61	20,345.86
Interest receivable		348.35
		$ 34,811.09

DECEMBER 31, 1938

ENDOWMENT FUND RESERVES

Endowment fund reserve—General		$2,000,000.00	
Endowment fund reserve—For upkeep of plant		419,419.96	
		$2,419,419.96	
Add:			
Realized net gain on securities called or sold	$19,406.44		
Reserve for amortization of bond premiums	6,265.97	25,672.41	$2,445,092.37
Reserve Fund	$30,000.00		
Less:			
Adjustment occasioned by sale of Imco Participating Certificates	6,604.43	$ 23,395.57	
Add—Reserve fund income		3,449.07	26,844.64
			$2,471,937.01

PLANT FUND RESERVES

Plant fund reserve—General	$ 607,642.13	
Plant fund reserve—From current account	27,806.71	$ 635,448.84
Reserve for depreciation (reserve for periodic replacements)		33,648.02
		$ 669,096.86

CURRENT LIABILITIES AND SURPLUS

Accounts payable		$ 8,110.44
Reserve for "working balance"		5,000.00
Current surplus:		
Balance at December 31, 1937	$24,592.26	
Less—Excess of expenses over income for the year ended December 31, 1938	2,891.61	21,700.65
		$ 34,811.09

STATEMENTS OF INCOME FROM ENDOWMENT FUND INVESTMENTS AND CURRENT ASSETS, AND EXPENSES APPLICABLE THERETO, INCLUDING EXPENDITURES FOR PERMANENT PLANT ADDITIONS

FOR THE YEAR ENDED DECEMBER 31, 1938 AND FOR THE YEAR ENDED DECEMBER 31, 1937

		Year Ended December 31, 1938			Year Ended December 31, 1937		
Income:							
Income from endowment funds:							
Interest		$63,530.07			$64,696.11		
Dividends		46,154.77			56,317.01		
			$109,684.84			$121,013.12	
Less—Custodian fees and expenses			1,490.73			1,468.73	
			$108,194.11			$119,544.39	
Carnegie Corporation grant for operating expenses			1,000.00			—	
Total income				$109,194.11			$119,544.39
	Budget						
Expenses:							
Upkeep of plant:							
Upkeep of buildings and grounds	$ 6,425.00	$ 8,893.99			$ 8,116.00		
Upkeep of "Atlantis"	9,000.00	12,629.42			12,978.78		
Upkeep of "Asterias"	150.00	120.36			52.62		
Insurance	6,155.99	5,833.90			5,816.74		
Depreciation	4,800.00	4,800.00			4,800.00		
	$ 26,530.99		$ 32,277.67			$ 31,764.14	
Operating Expenses:							
Operation of "Atlantis"	$ 29,350.00	$29,919.11			$28,901.55		
Operation of "Asterias"	900.00	1,289.44			900.58		
Scientists' salaries	28,679.00	26,875.51			27,200.14		
Scientific supplies and equipment	4,500.00	6,699.13			4,516.44		
Traveling expenses	565.00	856.25			424.56		
Publications	3,500.00	2,917.06			2,327.72		
Administration	8,825.00	7,497.85			7,098.19		
Amortization of bond premiums	2,000.00	1,586.32			1,800.63		
Contribution to retirement fund	1,784.60	1,567.38			1,771.19		
Not allocated	265.41	—			—		
	$ 80,369.01		79,208.05			74,941.00	
Total expenses	$106,900.00		$111,485.72			$106,705.14	
Expenditures for permanent plant additions:							
Additions to library	600.00		600.00			600.00	
	$107,500.00			112,085.72			107,305.14
Excess of expenses over income for 1938				*$ 2,891.61*			
Excess of income over expenses for 1937							$ 12,239.25

IV. NINTH ANNUAL REPORT OF THE DIRECTOR FOR THE YEAR 1938

BY HENRY B. BIGELOW

Equipment

New shelving for the storage of publications was installed; a room has been set apart for the storage of plankton samples which are now beginning to assume formidable proportions; and the U. S. Coast and Geodetic Survey has reconstructed the tide gauge house on the dock under a grant from the Public Works Administration.

Our work in physical oceanography has now reached a point where it is necessary to anchor "Atlantis" in deep water with our trawling wire, and after some experiment, a gallows has been installed at the bow for this purpose.

While "Atlantis" was in the shipyard last November and December, the ballast was removed in the after hold, the skin cleaned and covered with bitumastic before restowing; the port anchor chain was regalvanized; the linoleum in two cabins was replaced and wooden gratings were substituted for the lineoleum in the deck laboratory; and a new battery set was installed.

The engine of "Asterias" was thoroughly overhauled and certain repairs made to the hull.

The most important additions to our scientific equipment during the past year have been 30,000 feet of new ½ inch steel trawling wire and 22,000 feet of hydrographic wire; several "Otter" and "Blake" trawls; two Monaco deep sea fish traps; a "Hjort" bottom sampler and two other similar, but simpler, bottom samplers; a set of bolting silk plankton nets; 5 flow meters for plankton nets; ten new deep sea thermometers; a microscope; and a drill press for the machine shop. The recording current meter, on the development of which Professor Watson has been employed, has received a first successful trial on "Atlantis."

Library

Our contribution of $600. to the library of the Marine Biological Laboratory allowed subscription to 41 current journals and monographs, the completion of two back sets, purchase of six books, and the binding of 45 volumes. Seven current journals were received as gifts, while 70 current journals were added by exchange, and about 390 other reprints and pamphlets were placed in the library.

Personnel

The only changes in the scientific staff have been the appointments of Dr. Raymond B. Montgomery as Junior Oceanographer, Mr. D. Q. Anderson as Bacteriological Technician and Dr. Sidney Hsiao as Technician in Physical Oceanography; and the resignation of Mr. Dayton E. Carritt as Chemical Technician.

The following have worked at the laboratory during the past summer under fellowships: David D. Bonnet, Edward M. Brooks, Coit M. Coker, Robert H. Hay, Clifford E. Herrick, Jr., Charles W. Hock, Lois C. Lillick, Frances L. Parker, Robert C. Stauffer, Harold A. Thomas, Jr., Th. von Brand and Talbot H. Waterman, the latter carrying on his work at the Bermuda Biological Station. Twelve assistants have worked for various members of the staff during part of the year. There have been three volunteer workers.

The following visiting investigators have worked at the Laboratory during the year: Dr. A. A. Abramowitz, Mr. Gardner Emmons, Dr. Maurice Ewing, Dr. Stina Gripenberg, Dr. Frederick L. Hisaw, Dr. B. H. Ketchum, Dr. Clinton M. Osborn, Dr. G. H. Parker, Mr. Charles L. Schneider, Mr. A. F. Spilhaus, Dr. K. V. Thimann, Dr. George Wald, Dr. C. P. Winsor, Dr. E. F. Thompson and Mr. Herman Yagoda.

Through the generosity of a friend, the salary was supplied for the services of a skilled mechanic for the months of July and August.

The following institutions were represented during the year in the laboratory or on cruises of "Atlantis": Barat College, Barnard College, Bermuda Biological Station for Research, Harvard University, Lehigh University, Massachusetts Institute of Technology, New York University, Princeton University, Queen's University, Rutgers University, U. S. Coast Guard, U. S. Navy, U. S. Weather Bureau, University of North Carolina and University of Pennsylvania.

There have been no changes in the officers of "Atlantis." "Asterias" was in charge of Captain Norman Cleaves, assisted by William Butcher, William Glidden and Charles Taylor.

Travel

Professor Iselin visited the Bermuda Biological Station in April; Dr. Seiwell spent most of the winter working at Scripps Institution of Oceanography; Dr. Clarke spent the summer at the Trout Lake Laboratory of the University of Wisconsin; Professor Waksman attended a soil science congress in Finland, afterwards making other European visits in connection with his researches. And Dr. Montgomery went to Europe, in September, under a National Research

Council Fellowship, to work first with Professor Defant, at the Institut für Meereskunde, in Berlin, and later to visit other oceanographic laboratories.

Publications

Volume V, No. 4, and Volume VI, Nos. 1 and 2, of Papers in Physical Oceanography and Meterology were printed.

The following contributions were published during the year:

No. 136. Schalk, Marshall. A Textural Study of the Outer Beach of Cape Cod, Massachusetts. Jour. Sedimentary Petrology, Vol. 8, No. 2, pp. 41–54. 1938.

No. 147. Bigelow, Henry B. Plankton of the Bermuda Oceanographic Expeditions. VIII. Medusae taken during the Years 1929 and 1930. Zoologica, Vol. XXIII, Part 2. No. 5, pp. 99–189. 1938.

No. 152. Seiwell, H. R. and Gladys Eddy Seiwell. The Sinking of Decomposing Plankton in Sea Water and its Relationship to Oxygen Consumption and Phosphorus Liberation. Proc. Am. Philos. Soc., Vol. 78, No. 3, pp. 465–481. 1938.

No. 154. Soule, Floyd M. Oceanography. Excerpt from International Ice Observation and Ice Patrol Service in the North Atlantic Ocean, Season of 1936. U. S. Coast Guard Bull., No. 26, pp. 33–82. 1938.

No. 159. Redfield, Alfred C. and Ancel B. Keys. The Distribution of Ammonia in the Waters of the Gulf of Maine. Biol. Bull., Vol. LXXIV, No. 1, pp. 83–92. 1938.

No. 160. Waksman, Selman A., Margaret Hotchkiss, Cornelia L. Carey and Y. Hardman. Decomposition of Nitrogenous Substances in Sea Water by Bacteria. Jour. Bacteriology, Vol. 35, No. 5, pp. 477–486. 1938.

No. 161. Waksman, Selman A. and Unto Vartiovaara. The Adsorption of Bacteria by Marine Bottom. Biol. Bull., Vol. LXXIV, No. 1, pp. 56–63. 1938.

No. 162. Seiwell, H. R. Application of the Distribution of Oxygen to the Physical Oceanography of the Caribbean Sea Region. Papers in Physical Oceanography and Meteorology, Vol. VI, No. 1, pp. 1–60. 1938.

No. 163. Von Brand, Theodor. Quantitative Determination of the Nitrogen in the Particulate Matter of the Sea. Jour. d. Conseil, Vol. XII, No. 2, pp. 187–196. 1938.

No. 165. Waksman, Selman A. and Margaret Hotchkiss. On the Oxidation of Organic Matter in Marine Sediments by Bacteria. Sears Found. Jour. Mar. Res., Vol. I, No. 2, pp. 101–118. 1938.

No. 166. Clarke, George L. Seasonal Changes in the Intensity of Submarine Illumination off Woods Hole. Ecology, Vol. 19, No. 1, pp. 89–106. 1938.

No. 167. Spilhaus, Athelstan F. A Bathythermograph. Sears Found. Jour. Mar. Res., Vol. I, No. 2, pp. 95–100. 1938.

No. 168. Clarke, George L. Light Penetration in the Caribbean Sea and in the Gulf of Mexico. Sears Found. Jour. Mar. Res., Vol. I, No. 2, pp. 85–94. 1938.

No. 169. Stetson, Henry C. Present Status of the Problem of Submarine Canyons. Proc. Amer. Philos. Soc., Vol. 79, No. 1, pp. 27–33. 1938.

No. 170. Montgomery, R. B. Fluctuations in Monthly Sea Level on Eastern U. S. Coast as Related to Dynamics of Western North Atlantic Ocean. Sears Found. Jour. Mar. Res., Vol. I, No. 2, pp. 165–185. 1938.

No. 171. Iselin, C. O'D. The Influence of Fluctuations in the Major Ocean Current on the Climate and the Fisheries. The Collecting Net, Vol. XIII, No. 7, pp. 1–4. 1938.

No. 172. Ketchum, Bostwick H. and Alfred C. Redfield. A Method for Maintaining a Continuous Supply of Marine Diatoms by Culture. Biol. Bull., Vol. LXXV, No. 1, pp. 165–169. 1938.

No. 174. Leavitt, Benjamin B. The Quantitative Vertical Distribution of Macrozoöplankton in the Atlantic Ocean Basin. Biol. Bull., Vol. LXXIV, No. 3, pp. 376–394. 1938.

No. 175. Rakestraw, Norris W. and Victor M. Emmel. The Solubility of Nitrogen and Argon in Sea Water. Jour. Phys. Chem., Vol. 42, No. 9, pp. 1211–1215. 1938.

No. 176. Welsh, J. H. and F. A. Chace, Jr. Eyes of Deep-Sea Crustaceans II. Sergestidae. Biol. Bull., Vol. LXXIV, No. 3, pp. 364–375. 1938.

No. 177. Seiwell, H. R. Eddy Diffusion at Mid-Depths in the Caribbean Sea Region. Jour. d. Conseil, Vol. XIII, No. 2, pp. 155–162. 1938.

No. 178. Stetson, H. C. The Sediments of the Continental Shelf off the Eastern Coast of the United States. Papers in Physical Oceanography and Meteorology, Vol. V, No. 4, pp. 1–48. 1938.

No. 179. Parr, Albert Eide. Further Observations on the Hydrography of the Eastern Caribbean and Adjacent Atlantic Waters. Bull. Bingham Oceanographic Coll., Vol. 6, Art. 4, pp. 1–29. 1938.

No. 180. Iselin, C. O'D. A Promising Theory Concerning the Causes and Results of Long-Period Variations in the Strength of the Gulf Stream System. Trans. Am. Geophys. Union, Nineteenth Annual Meeting, pp. 243–244. 1938.

No. 181. Seiwell, H. R. Use of Non-Conservative Properties of Sea Water to Physical Oceanographical Problems. Nature, Vol. 142, p. 164. 1938.

No. 182. Rakestraw Norris W. and Victor M. Emmel. The Relation of Dissolved Oxygen to Nitrogen in Some Atlantic Waters. Sears Found. Jour. Mar. Res., Vol. I, No. 3, pp. 207–216. 1938.

No. 183. Johnson, W. H. The Effect of Light on the Vertical Movements of *Acartia clausi* (Giesbrecht). Biol. Bull., Vol. LXXV, No. 1, pp. 106–118. 1938.

No. 185. Rossby, C.-G. On the Mutual Adjustment of Pressure and Velocity Distributions in Certain Simple Current Systems, II. Sears Found. Jour. Mar. Res., Vol. I, No. 3, pp. 239–263. 1938.

No. 186. Seiwell, H. R. Über die ganz- und halbtägige Mondkomponente der internen Wellen im westlichen Nordatlantischen Ozean. Annalen der Hydrographie u. maritimen Meteorologie, Heft X, pp. 485–487. 1938.

No. 188. Carey, Cornelia L. The Occurrence and Distribution of Nitrifying Bacteria in the Sea. Sears Found. Jour. Mar. Res., Vol. I, No. 4, pp. 291–304. 1938.

No. 189. Lillick, Lois C. Preliminary Report of the Phytoplankton of the Gulf of Maine. The Amer. Midland Nat., Vol. 20, No. 3, pp. 624–640. 1938.

No. 190. Montgomery, R. B. Circulation in Upper Layers of Southern North Atlantic Deduced with Use of Isentropic Analysis. Papers in Physical Oceanography and Meteorology, Vol. VI, No. 2, pp. 1–55. 1938.

No. 198. Clench, W. J. and C. G. Aguayo. Notes and Descriptions of New Species of Calliostoma, Gaza and Columbarium (Mollusca); Obtained by the Harvard-Havana Expedition off the Coast of Cuba. Mem. Soc. Cub. Hist. Nat., Vol. 12, No. 5, pp. 375–384. 1938.

No. 200. Bermúdez. Pedro J. Resultados de la Primera Expedicion en las Antillas del Ketch Atlantis bajo los Auspicios de las Universidades de Harvard y Habana. Mem. Soc. Cub. Hist. Nat., Vol. 12, No. 5, pp. 385–388. 1938.

Coöperation

The physical investigations from the coast out to Bermuda, in coöperation with Bermuda Biological Station, have now fallen in place as one of the regular items of our activities and seven profiles were run during the past year, in one of which Dr. E. F. Thompson, hydrologist of the Bermuda Station, participated. "Atlantis" was also able to take Drs. Garstang and Gurney from Bermuda for some deep sea towing and occupied a line of stations to obtain data for Dr. Thompson around the islands. The possibility that mutual shifts in mean sea level on the two sides of an ocean current may give a measure of the velocity of the latter, has recently received considerable attention. In the hope of reaching a solution, a tide gauge, supplied by the U. S. Coast and Geodetic Survey, was installed by Mr. Woodcock at Cat Cay in the Bahamas last winter, to allow comparison of the marigrams obtained there with those from Miami on the opposite side of the Straits of Florida. Mr. Woodcock also assisted in setting up a tide gauge at Bermuda.

In September "Atlantis" took Dr. Ewing on another cruise for further tests of his seismic apparatus in connection with the investigations mentioned in earlier reports, in which we have coöperated with Lehigh University and the Geological Society of America. Cores, in localities where the bottom deposits are not stratified, were also obtained for the Carnegie Institution, for studies in magnetism.

During the winter "Atlantis" in charge of Mr. William C. Schroeder, accompanied by Drs. Luis Howell Rivero, Pedro J. Bermúdez and Carlos Guillermo Aguayo from the University of Havana, carried out a biological survey of the mid-depth bottoms around Cuba in coöperation with Harvard University and the University of Havana, the collecting gear being provided by the two institutions. We have to thank the University of Havana for courtesies extended while in Cuba, and the U. S. Navy for assistance while the ship was in Guantanamo.

While it is still too early for accurate appraisal of the results, we can say that in spite of much difficulty with bad bottom, an astonishingly large collection was secured, especially of fishes, crustacea, echinoderms and mollusks, including a large number of new species. Reports on the various groups are now in preparation by several specialists with a view to publication.

In April and May "Atlantis" made a cruise to Georges Bank, for haddock investigations for the U. S. Bureau of Fisheries, in charge of Mr. John Webster of the Bureau.

Finally "Asterias" collected diatoms in large quantity (about 12 liters of diatom sludge), near Gloucester, during April, under a grant from the Carnegie Corporation, for use by Professor Hans Clarke in investigations which have already revealed an unusual biochemical composition, possibly explaining reactions of great theoretic and economic importance.

Field Work

Operations of "Atlantis" for the year 1938:

Cruise 74: January–April; circumnavigation of Cuba.

Cruise 75: April–May; Georges Bank.

Cruise 76: May; off Montauk Point.

Cruise 77: May–July; Bermuda.

Cruise 78: July–August; south of Montauk Point.

Cruise 79: August; Gulf of Maine.

Cruise 80: August–September; across the Gulf Stream on the Montauk Point-Bermuda line.

Cruise 81: September; south of Woods Hole

Cruise 82: September–October; Bermuda

Summary of observations:

Total distance sailed, miles	14,763
Number of days at sea	246
Deep hydrological stations	164
Shallow hydrological stations	42
Serial temperature lowerings for internal waves	272
Plankton hauls	391
Bottom trawl hauls	204
Bottom samples	37

"Asterias" was in commission from early April when she spent six weeks collecting diatoms near Gloucester, to September. During the summer she was employed as usual, on short trips near shore and in the Gulf of Maine.

Staff Meetings

Nine staff meetings were held at which the speakers were Norris W. Rakestraw, Clifford E. Herrick, Jr., Cornelia L. Carey, Mary Sears, Charles E. Renn, C.-G. Rossby, Columbus O'D. Iselin, G. H. Parker, A. Abramowitz, C. M. Osborn, D. Q. Anderson, Wm. C. Schroeder, Stina Gripenberg and E. E. Watson.

A seminar was also held weekly by the various workers in physical oceanography.

Scientific Program

The chief lines of investigation in which the Institution is engaged may be summarized as follows:

Physical oceanography and meteorology

Internal waves. The subject of internal waves has been much to the fore of late. In June Dr. Seiwell occupied a fourteen-day station, between Bermuda and the Gulf Stream, on "Atlantis," taking repeated observations on temperature and salinity at close vertical intervals.

An analysis of the effect of vertical movements on temperature, salinity, dynamic topography, and related characteristics is under way, together with a theoretical investigation of the mechanism involved. And a preliminary report on the 12 and 24 lunar hour components of vertical motion, as shown at an eight day "Atlantis" station in 1937 has been published by Dr. Seiwell. Examination of the effect of submarine waves on calculations of dynamic topography is also in progress.

Synoptic studies. Two reports have been published, one by Dr. Montgomery on the circulation of the upper sub-surface layers of the southern North Atlantic deduced chiefly by the use of isentropic analysis, the other by Dr. Seiwell on the distribution of oxygen in the Caribbean sea region. Dr. Seiwell is also extending his studies of the minimum oxygen layer to a consideration of its relation to a nearly constant density surface to the South Atlantic, Eastern Pacific, and Indian Oceans. And one of our fellowship holders, Mr. Coit M. Coker, has nearly completed a report on the relation of the minimum concentration of oxygen in the Caribbean to other chemical and physical properties of the water.

Professor Iselin has made good progress in his studies of the scheme of circulation in the waters along the continental slope of Northeastern America, especially of the mixing processes along the northern edge of the Gulf Stream; also of the diurnal and seasonal thermal cycle in the surface layer. And a large body of data has been accumulated as to the seasonal and annual changes in strength of the Gulf Stream System, on the cruises of "Atlantis," in coöperation with the Bermuda Laboratory.

Mr. Soule's work on the Ice Patrol, including 4 current surveys of this critical region, yielded valuable evidence as to the depth of the most nearly motionless level beneath the Atlantic current and as to the direction of flow of the deep counter current.

Professor Watson's calculations of dynamic conditions in the

Gulf of Maine at all seasons of the year have yielded a series of pictures showing the seasonal changes and the interchanges of water at certain times with the neighboring Scotian banks and with the slope water beyond Georges Bank. With the calculations completed, it is hoped that it will soon be possible to publish an account of the most recent ideas about the circulation in the Gulf of Maine and of coastal waters in general.

Theoretical studies. Professor Rossby completed the second part of his theoretical study of the adjustment of the internal mass distribution in the ocean to changes in the current distribution caused by changes in the wind distribution at the sea surface, indicating that dynamic changes in the interior of the ocean, that accompany large scale changes in the currents at the sea surface, must be felt all the way down to the bottom, as very slow turbulent horizontal motions. This tentative conclusion is now being tested on oxygen, and if verified is likely to have a profound influence on present views as to circulation in the deep oceans.

Professor Spilhaus investigated the origin of the apparently retrograde eddies observed on the edge of the Gulf Stream by a study of frictionally driven eddies in the air, also by comparison of observed motion with geostrophic potential gradient on isentropic surfaces. And he has continued his examination of circulatory patterns set up in a rotating tank.

Instrumental. The recording current meter which was built last summer under Professor Watson's supervision was tested, successfully, on "Atlantis" to a depth of 250 meters. And the automatic recording apparatus, which goes on the ship, was perfected.

Professor Spilhaus has likewise developed two instruments for the purpose of speeding up observations in the surface layers of the ocean; namely a Bathythermograph, and a pressure operated Multiple Sea Sampler. The rapid technique made possible by these instruments will, it is hoped, make a closer approach to synoptic observations practicable.

Biological-chemistry of sea water

The more strictly chemical division of the Institution has carried on four lines of work during the last year:

1. A seasonal survey of the waters between Woods Hole and Bermuda, in coöperation with the hydrographic and biological work on this line of stations, the goal being a complete chemical picture for the annual cycle.

2. A study of dissolved gaseous nitrogen and argon in sea water. Two papers on this subject were published.

3. A study of dissolved helium and neon in sea water, to determine whether, indeed, the distribution of these gases is irregular, as has been previously reported.

4. Continued experimental decomposition and regeneration of nitrogenous organic matter in the sea.

Professor Redfield and Dr. Keys have also published an account of the ammonia content of the waters of the Gulf of Maine; Professor Redfield of the phosphorus. Professor von Brand made analyses of the nitrogen content of the particulate matter in samples secured at six stations during the Bermuda program, also of decomposing diatoms. And Dr. and Mrs. Seiwell continued their study of the settling velocities of decomposing particles in sea water, using an apparatus designed to measure the effects of compression and of stratification of the water column.

Marine bacteriology

Most of the projects in bacteriology have a common goal, namely the investigation of the decomposition of organic matter in the sea.

In connection with Mr. Anderson's studies on organic matter in the various strata of marine sediments and its availability for bacterial decomposition, cores were collected with a newly devised sampler at various stations in the Gulf of Maine and in the vicinity of Woods Hole. Professor Carey investigated the distance, down into the mud, to which nitrifying organisms exist, while Dr. Hock studied the rate of decomposition of chitin in mud, in sand, and in sea water, as well as the morphological and physiological characteristics of pure cultures of chitin-attacking bacteria.

Dr. Renn continued his studies of the availability of nitrogen in the sea, in conjunction with Professors Rakestraw and von Brand, and is engaged on the development of a respirometer for measuring the rate of oxygen utilization by bottom sediments.

Professor Thimann began a study of the conditions governing the precipitation of calcium carbonate from sea water, and of the rôle of bacteria in promoting such precipitation.

Dr. H. A. Thomas tested the applicability, to salt water, of the methods in use for the detection of sewage pollution in fresh water, using mud and water samples collected at several stations along a line beginning in New Bedford harbor, and extending about 15 miles into Buzzards Bay.

Physiology of marine organisms

Physiological work, of the more strictly oceanographic sort, was devoted, as usual, to the conditions of life of copepods and diatoms.

Mr. Bonnet measured the oxygen consumption of copepods, particularly *Calanus finmarchicus*, using a Dixon constant-pressure respirator adapted for use with small animals, with parallel measurements by the Winkler method for comparison with previous work upon the oxygen consumption of copepods.

Under Professor Redfield's direction, Dr. Ketchum developed a method for growing pure cultures of the marine diatom *Nitzschia Closterium* in large quantities on which the formation of various organic compounds of phosphorus in the cell was studied, the investigation also including analyses of fat, of sugar and of protein formation by cells grown under various environmental conditions.

Mr. Stauffer determined, for this same diatom, the intensity of illumination at which photosynthesis just balances respiration, an important point in diatom economy because light intensity is the principle factor determining the greatest depth to which diatoms can grow and contribute to the economy of the sea.

Dr. Osborn, under Professor G. H. Parker's supervision, studied the physiological mechanism involved in the color adaptation of several species of local flat fishes to black and white backgrounds, and to light and dark, the behavior of innervated and denervated areas of their skins, and their responses to a variety of drugs and hormones.

Professor Hisaw and Dr. Abramowitz completed the investigation, which was begun last summer, of the normal reproductive cycle of the smooth dogfish, *Mustelis canis;* continued their observations on the more complicated reproductive cycle of the spiny dogfish, *Squalus acanthius;* and studied the seasonal distribution of estrogenic hormone in the latter species.

Dr. George Wald, on a short visit, continued his work on the distribution of vitamins A_1 and A_2 among liver oils and eye tissues of various local fishes.

Plankton studies

Dr. Lillick worked on a general account of the phytoplankton of the Gulf of Maine, based on all available information, of which her own investigations of collections made on "Atlantis" cruises form the chief item; and Professor Redfield completed a study of the distribution of the pteropod, Limacina, in relation to the circulation of the Gulf of Maine.

Mr. Coker made a quantitative analysis of the vertical distribution of the chaetognaths previously collected by the "Atlantis" in deep water at stations along the profile between Woods Hole and Bermuda. Dr. Winsor continued his statistical examination of the results of simultaneous and successive hauls of plankton nets of various types, with a view to establishing and evaluating the variability arising from different causes. And Dr. Sears and I completed our report on quantitative distribution of the zoöplankton of the continental shelf between Cape Cod and Chesapeake Bay.

Finally, in connection with Dr. Clarke's studies of planktonic production in different ocean waters, 7 surveys were made on the Montauk-Bermuda line, including 371 hauls of various kinds at 60 stations. Analysis of the catches is now in progress.

Fisheries biology

Besides the Fisheries cruise mentioned elsewhere (p. 13), Mr. William Gosline studied the abundance of different year classes, and the growth types, among Canadian herring, in relation to the problem of local races, under Mr. Schroeder's supervision.

Submarine geology

Mr. Stetson, in continuation of his studies on marine sediments, obtained 23 additional long cores with the Piggot gun, from "Atlantis" at representative localities along the continental slope, between the offings of New York and of Chesapeake Bay, both in the valley-bottoms, and on the intervening ridges. And Dr. Joseph A. Cushman and Miss Frances L. Parker, in their study of the faunal ranges of the foraminifera along the eastern coast of the United States, have practically completed the mechanical work of sorting the samples from the seven northern traverses, while the species of two of these have been studied in detail.

V. STAFF

(As of December 31, 1938)

Henry B. Bigelow, Professor of Zoölogy, Harvard University, Director

Cornelia L. Carey, Assistant Professor of Botany, Barnard College, Research Associate in Marine Bacteriology

George L. Clarke, Tutor and Instructor in Biology, Harvard University, Junior Biologist

Columbus O'D. Iselin, Assistant Professor of Physical Oceanography, Harvard University, and Assistant Curator of Oceanography, Museum of Comparative Zoölogy, Research Associate in Physical Oceanography

Raymond B. Montgomery, Junior Oceanographer

A. E. Parr, Director of Peabody Museum and Curator of the Bingham Oceanographic Collection, Yale University, Research Associate in Oceanography

Norris W. Rakestraw, Associate Professor of Chemistry, Brown University, Research Associate in Physical Chemistry

Alfred C. Redfield, Professor of Physiology, Harvard University, Research Associate in Biology

C. E. Renn, Tutor in Biology and Instructor in Sanitary Engineering, Harvard University, Junior Marine Bacteriologist

C.-G. Rossby, Professor of Meteorology, Massachusetts Institute of Technology, Oceanographer

H. R. Seiwell, Investigator in Oceanography

Floyd M. Soule, Senior Physical Oceanographer, U. S. Coast Guard, Research Associate in Oceanography

Athelstan F. Spilhaus, Assistant Professor of Meteorology, New York University, Investigator in Physical Oceanography

Henry C. Stetson, Research Associate in Paleontology, Museum of Comparative Zoölogy, Research Associate in Submarine Geology

Selman A. Waksman, Microbiologist, New Jersey Agricultural Experiment Station, Marine Bacteriologist

E. E. Watson, Assistant Professor of Physics, Queen's University, Research Associate in Physical Oceanography

Captain Sir Hubert Wilkins, Honorary Research Associate in Oceanography

David Q. Anderson, Bacteriological Technician

Dean F. Bumpus, Biological Technician

Sidney T. C. Hsiao, Technician in Physical Oceanography

Alfred Woodcock, Oceanographic Technician

William C. Schroeder, Business Manager

Mrs. Virginia Walker Smith, Secretary and Administrative Assistant

William Schroeder, Superintendent of Buildings and Grounds

APPENDIX

Reports of progress by investigators working at the Institution during 1938.

ZOÖPLANKTON STUDIES

HENRY B. BIGELOW AND MARY SEARS

Our report on the quantitative distribution of the Zoöplankton of the continental shelf waters, Cape Cod to Chesapeake Bay, was completed for publication.

THE RESPIRATION OF *CALANUS FINMARCHICUS*

DAVID D. BONNET

A study of the respiration of *Calanus finmarchicus* at different temperatures was made, using a manometric respirometer of the Dixon-Haldane constant pressure type. It was found that the oxygen consumption of this copepod from local waters was of the same order of magnitude as that of copepods from European waters as determined by Marshall, Nicholls, & Orr at Plymouth, in 1935, with values ranging from 0.32 at 5° C. to 0.91 at 17° C. (expressed in cc. O_2/hour/1000 animals).

LIGHT PENETRATION AND TRANSPARENCY OF SEA WATER; ZOÖPLANKTON STUDIES

GEORGE L. CLARKE

1. Measurements of light penetration were made at intervals at standard stations in coastal water, in continental slope water, and in Sargasso water using instruments sensitive respectively to the whole visible spectrum and to the green wave lengths only. The three localities differed sharply in transparency, but the water at each was found to be optically homogeneous. Seasonal differences were greatest in the coastal water. Samples of water from these three stations and from three others near Woods Hole were also analyzed in the monochromator at the University of Wisconsin both before and after Berkefeld filtering. The absorption of filtered sea water from the off-shore stations was found to be practically identical with distilled water. Coastal water was shown to contain a filter-passing material which exerts a highly selective action on light and which is not present in off-shore waters.

2. The influence of temperature and of food on the survival and growth of the copepod *Calanus finmarchicus* was investigated in a series of laboratory experiments. At 3° C. survival was good, but the

growth of the animals was retarded regardless of the amount of food provided. At 6° C. and 9° C. survival was inferior, but a larger amount of successful moulting occurred, and both were directly influenced by food.

3. A plankton sampler has been developed, in which a precise measure of the amount of water strained by the net is given by a volume meter, and five have been put into operation. The samplers have proven useful for quantitative zoöplankton studies, particularly in coastal water where animals are abundant, and also for detecting differential currents in subsurface strata.

4. The zoöplankton of three typical areas of the ocean was studied throughout the year by means of net hauls and collections made with the plankton sampler from the "Atlantis" on her sections from Montauk Point toward Bermuda. Standard stations were made in the center of the coastal water, in the continental slope water, and in the Sargasso water and six subsidiary stations were interposed. Qualitative and quantitative analysis of the material has been commenced. Since the section was traversed nine times, it should be possible to detect the seasonal variations in each area as well as the particular differences between the areas.

PHYSIOLOGY OF REPRODUCTION IN THE DOGFISHES, *MUSTELIS CANIS* AND *SQUALUS ACANTHIUS*

F. L. HISAW AND A. A. ABRAMOWITZ

The account, presented in our last report, of the normal reproductive cycle of the smooth dogfish was fully confirmed. One event—that concerning ovulation—which had not been studied was worked out. Ovulation does not occur completely without copulation.

Data were accumulated on the normal cycle of the spiny dogfish, dealing chiefly with the growth of the embryo and ovogenesis. The data we have at present indicate a gestation period of 22 months.

Considerable more tissue for chemical work on the naturally occurring hormones in the gonads of both the spiny and the smooth dogfishes was accumulated.

In the smooth dogfish, attempts made the previous summer to stimulate the reproductive tract of immature specimens by injections of pure sex hormones were unsuccessful. We tried again with an improved technique and obtained very successful results. In male yearlings, male hormone accelerated the growth of the claspers while in female yearlings, female sex hormone produced a maturation of the genital tract equivalent to that seen in a normal three year old specimen.

HYDROLOGICAL INVESTIGATIONS

C. O'D. ISELIN

In preparing a report on the "Atlantis" surveys of the eastern slope water area, it has become necessary to examine critically the various indirect methods of determining subsurface current direction. This has led to some clarification of the basic assumptions on which these methods depend and to a better understanding of their reliability. It has also led to the conclusion that as soon as possible a new instrumental technique must be developed, for it has become evident that the ordinary water-bottle observations are not capable of explaining the large scale mixing processes along the borders of such a current as the Gulf Stream. Besides new instruments, it will probably become necessary to enlist the coöperation of at least one additional ship, for it is probable that the "Atlantis," working alone, will not be able to adequately survey the frictionally-driven eddies which often are met with north of the Gulf Stream.

The routine observations on the Montauk Point-Bermuda line now provide 16 sections for a study of the variability of the Gulf Stream. A preliminary report on this material was sent to the Bermuda Oceanographical Committee of the Royal Society of London in December. Dr. Thompson has spent a good deal of time at Woods Hole during the past year and has made considerable progress with the accumulated observations from the neighborhood of Bermuda. In recent months the "Culver" has been able to take over the local routine observations.

During the past summer Mr. E. M. Brooks made a computation of the surface transport resulting under certain assumptions from the mean winter winds over the North Atlantic. He also drew up a report on the instrumental requirements of the proposed program for measuring the friction between the winds and the sea surface. This information, along with other suggestions, has been forwarded to the Committee on Questions of the Interaction between the Sea and the Atmosphere of the International Union of Geodesy and Geophysics.

PHYTOPLANKTON INVESTIGATIONS

LOIS C. LILLICK

Large-scale culturing of the diatom *Nitzschia Closterium* was carried on under Professor Redfield's supervision, and experiments were made with Professor Rakestraw on the growth of diatoms in recrystallized sea salts. A preliminary examination was made of recently collected phytoplankton from the continental slope and Gulf

Stream. Tables of the phytoplankton collected in past years by "Atlantis" in the Gulf of Maine were published. And a general report on the seasonal and regional distribution of pelagic plants, in the Gulf, was brought nearly to completion.

STUDIES OF OCEANIC CIRCULATION BASED ON ISENTROPIC ANALYSIS

RAYMOND B. MONTGOMERY

A study of the circulation in the upper strata of the North Tropical Atlantic based on isentropic analysis was completed and published. This work was continued in Berlin, with Professor Defant, at the Institut für Meereskunde.

THE PHYSIOLOGY OF COLOR CHANGE IN FLATFISHES

CLINTON M. OSBORN

Experiments on the mechanisms of color change were made on the winter flounder, *Pseudopleuronectes americanus*, on the sand dab, *Lophopsetta maculata*, and on the summer flounder, *Paralichthys dentatus*. All of these species adapt markedly in shade to black or white illuminated backgrounds. Spots of contrasting shade characteristic of each species exhibit specific background responses.

Blinding in Pseudopleuronectes and Lophopsetta results in an intermediate brown shade quite free from spots.

Denervated areas darken in pale animals but subsequently fade if constantly illuminated. Vigorous excitement causes marked pallor in denervated areas due presumably to an adrenalin-like substance in the blood. Adrenalin injections produce a similar pallor. Innervated areas in black-adapted fishes also pale temporarily following excitement and characteristic "spotting" responses are elicited. White-adapted fishes darken to excitement and exhibit dark local spots.

Extracts of the pituitary of *Paralichthys dentatus* contain melanophore-dispersing materials as evidenced by their darkening effects in test frogs and catfishes. Nevertheless, injections of relatively high doses of four different pituitary preparations failed to darken pale Pseudopleuronectes.

CHEMICAL INVESTIGATIONS

NORRIS W. RAKESTRAW

1. The data accumulated along the Montauk-Bermuda profile, mainly by the chemical technician, Mr. D. E. Carritt, on seven

cruises, now covers a full year's cycle, and provides material for a fairly comprehensive picture of the chemical changes in the three principal water masses between Woods Hole and Bermuda during the year.

2. The study of the decomposition and regeneration of nitrogenous organic matter, begun in 1936 in collaboration with Professor von Brand and Dr. Renn, has been considerably extended, and a paper combining results of 1937 with those of 1938 is now in preparation. In fifteen months' time it has been possible to carry out three successive cycles of decomposition and regeneration in the same water and to observe, both qualitatively and quantitatively, a number of factors influencing these changes. The influence of anaerobic conditions has been studied and the groundwork laid for a more thorough study of the rates at which the various changes take place under different conditions.

3. An investigation of the helium content of sea water, carried out principally by Mr. C. E. Herrick, has been practically finished. We were unable to confirm the earlier reports of a correlation between the oxygen minimum and a supposed helium minimum, and believe we can trace the earlier results to the technique used in carrying out the difficult and laborious analysis. Samples from two stations, both showing a very distinct oxygen minimum, indicated a practically constant helium distribution at all depths. Samples from the Pacific, which we had obtained for this work, had apparently stood too long before use, but we hope to get another set with which to corroborate the data from the Atlantic.

STUDIES ON THE BIOLOGY OF THE GULF OF MAINE, AND OF THE PHYSIOLOGY OF DIATOMS

ALFRED C. REDFIELD

The growing of diatoms and certain other algae in mass cultures at a rate sufficient to make possible a variety of studies on the biochemical processes of these forms was successful and was continued during the summer in collaboration with Drs. B. H. Ketchum and Lois Lillick.

Dr. Ketchum completed a study of the conditions controlling the removal of phosphate and nitrate from sea water by marine diatoms which is being prepared for publication.

A paper showing the important rôle which the drift water plays in the distribution of plankton in the Gulf of Maine, based on collections made by the "Atlantis" in 1933–34 was published.

Dr. Sidney Hsiao published two papers which constitute the first detailed studies of the phenomena of sex reversal in an oceanic pteropod.

THEORETICAL ANALYSIS

C.-G. ROSSBY

The theoretical work on the relation between velocity distribution and mass distribution was continued during the year and the second part of the report of this general investigation was published. The investigation continues.

STUDIES ON FISHES

WILLIAM C. SCHROEDER

1. *The Deep Water Fauna around Cuba.* During February and March "Atlantis" made a deep sea bottom trawling cruise around the island of Cuba to collect fishes and any other animals that could be obtained. A total of 103 hauls were made in depths ranging from 200 to 3886 meters. Of these 76 were successful. The gear consisted of 35 and 60-foot otter trawls, and 10 and 14 foot "Blake" trawls with rigid frame.

Particularly good catches were made between depths of 300 and 1500 meters. Estimates of the total catch include about 250 species of fishes together with about 800 species of invertebrates, exclusive of foraminifera and, of these thousand-odd species, about 100 are believed to be new.

The fishes are being studied by Dr. Luis Howell Rivero of Havana University, and myself, while the various other groups are in the hands of specialists.

2. *Migrations of Gulf of Maine Cod.* Studies of cod scales were made from time to time. This material was collected during the period 1924–1931 in the course of cod marking experiments and analyses thus far made indicate that stocks of fish such as those living on Georges Bank, Nantucket Shoals or along the coast of Maine have distinct types of scales. The Nantucket cod, for example, have an average of about 20 circuli in the first zone of growth whereas Georges cod may have an average of 18 and Maine cod only 15 or 16. If this difference of circulus count proves constant from year to year for various regions within the Gulf of Maine, it will provide a useful means for studying the migrations of the local stocks of cod.

3. *Herring.* Studies of herring scales were made during the summer by Mr. William Gosline who utilized material chiefly from Nova Scotia. Analyses were made of age classes and possible racial

groups but the results have not yet progressed far enough to yield definite results.

PROBLEMS OF OCEANIC CIRCULATION

H. R. SEIWELL

1. *Caribbean Sea.* Results of the reduction and study of oxygen data (obtained by "Atlantis" in 1933 and 1934) with reference to the circulation of this region, were published.

2. *Internal Waves.* Between January 1 and May 1, I was at the Scripps Institution of Oceanography to consult with Professors Sverdrup and McEwen on various theoretical and practical aspects of this problem. The continuous series of internal wave measurements obtained in 1937 have been partially analyzed, and a resumé of the harmonic constants for 24 and 12 lunar hour waves published. In June, two weeks of continuous observations were obtained from "Atlantis" in the same locality (northwest of Bermuda) as the 1936 and 1937 observations. In October the American Philosophical Society granted sufficient funds to employ a full time technician to assist with the problems. During the summer (assisted by Gladys Eddy Seiwell and later, by Andrew Stergion) research on the internal wave phenomenon was confined principally to practical aspects, with the object of estimating the significance of short period vertical oscillations of the water column in hydrostatic problems in the North Atlantic.

3. *Sinking of Organic Particles in Sea Water.* Results of laboratory studies on settling rates of decomposing organic matter in sea water were published in collaboration with Gladys Eddy Seiwell. During the summer technique was improved and measurements on the sinking of organic matter through a sea-water column of approximately six meters were continued.

4. *Origin of the Minimum Oxygen Concentration.* During the year progress was made on the problem, with the assistance of Coit M. Coker, by the investigation of density surfaces along which the principle minimum oxygen concentration has been observed.

5. *Applications of Methods of Mathematical Statistics to Oceanographic Data.* Systematic inquiry into methods adaptable for precise analysis of oceanographic field data was continued, in collaboration with Dr. George P. Wadsworth. Progress has been made chiefly in problems involving frequency distributions and correlation—a resumé of which was presented to the Statistical Congress in the autumn.

PHYSICAL OCEANOGRAPHY OF THE GRAND BANKS REGION AND LABRADOR SEA

FLOYD M. SOULE

The oceanographic section of U. S. Coast Guard Bulletin No. 27 (season of 1937) was completed for publication, with the development of evidence that a most nearly motionless level beneath the Atlantic Current east of the Grand Banks exists at a depth of about 2000 or 2500 meters and that below this level the deep water is in motion in a direction counter to the overlying Atlantic Current. The months of April, May, June and the first part of July were spent on the oceanographic vessel of the International Ice Patrol Force, the U.S.C.G. Patrol Boat *General Greene*, in the region of the Grand Banks, supplying topographic dynamic charts of the region to the Ice Patrol cutters *Tahoe* and *Pontchartrain*. During this period four current surveys of the critical area were made, the resulting charts being referred to the 1000-decibar surface although at most of the oceanographic stations the temperature and salinity measurements extended to a depth of 1400 meters where the depth of water permitted. In this work 268 oceanographic stations were occupied. Early in June a section was run from the Tail of the Grand Banks across both the Labrador and Atlantic Currents as far south as latitude 39° N. On this section temperature and salinity measurements extended to a depth of between 2000 and 2500 meters. From July 22 to August 17 serial observations of temperature and salinity were made at 39 oceanographic stations during a post-season cruise in the Labrador Sea, along sections (1) South Wolf Island, Labrador, to Cape Farewell, Greenland, (2) Longitudinal section from section (1) to Davis Strait Ridge, (3) On Davis Strait Ridge from the "West Ice" to Holsteinsborg, Greenland. Most of these stations were occupied from the surface to as near bottom as was practical.

In addition to the temperature and salinity observations, samples were collected for the determination of dissolved helium and oxygen from section (2) and from three stations in the middle of section (1); and 451 fathometer soundings were taken along these sections. These soundings have been corrected and tabulated and supplied to the U. S. Hydrographic Office and to the International Hydrographic Bureau. A continuous sonic sounding section was made along the continental shelf from Davis Strait to the Strait of Belle Isle to obtain information regarding the existence or non-existence of submarine canyons in this region.

FRICTIONALLY DRIVEN EDDIES

ATHELSTAN F. SPILHAUS

The attempt to obtain a representation and explanation of some impermanent current systems in the ocean (eddies in the neighborhood of the Gulf Stream) has proceeded along the following lines.

1. A detailed investigation of a large anticyclonic eddy in the atmosphere and its development under the influence of a frictional "drive," provided by the semipermanent stream of westerlies to the north, has been completed. This analysis in the atmosphere is of oceanographic interest in view of the implications it has regarding the possibility of a similar mechanism existing in the ocean in the neighborhood of a well developed permanent current. If such a mechanism exists it may provide some explanation for "retrograde" eddies in the vicinity of the Gulf Stream and further it means that the eddies will be temporary and that the main stream will suffer lateral displacements for comparatively short periods in accordance with their growth and decay. Patterns exhibiting some of the principal characteristics of the above system have been reproduced in the rotating tank.

2. The temporary nature of these eddies, which has of course been realized before, but which is emphasized by this work has created a need for a new instrumental technique in the form of rapid measuring instruments which will provide observations approximating more closely to synchronous conditions. Two instruments have been developed to this end: first, the Bathythermograph, for obtaining a continuous record of temperature and depth in the ocean and secondly, a companion instrument which may be described as a Pressure Operated Multiple Sea Sampler, for taking samples rapidly at various predetermined depths (pressures) for salinity and oxygen determinations. Preliminary tests of the Sea Sampler indicate that it will be ready in the near future for routine use. Further development of the Bathythermograph is proceeding. By the use of these instruments the time involved in the collection of data will be greatly reduced. Of particular significance in this connection is the fact that the use of these instruments will not require a hydrographic winch nor is it necessary to completely stop the vessel.

PHOTOSYNTHESIS OF ALGAE

ROBERT C. STAUFFER

Studies of the relation between the rate of photosynthesis and intensity of illumination were made on the diatom *Nitzschia Closterium* either grown in bacteria-free cultures in 500 cc. Erlenmeyer flasks, or in species-pure mass cultures in large glass cylinders. An attempt was made to obtain fresh diatoms from Vineyard Sound, but it did not prove possible to separate the phytoplankton from zoöplankton and bacteria in a state pure enough for experiment. For comparison with the cultured diatoms, two wild fixed algae were also used, one red, *Porphyra umbicalis*, and one green, *Ulva lactuca*. All experiments were carried out with Warburg manometers, using as a medium sea water saturated by an atmosphere with 5% CO_2.

For all three forms the compensation intensity at which oxygen production and respiration just balance fell within a narrow range not varying more than 40%. It was found that the cell concentrations affected the rate of photosynthesis noticeably when they ranged between 5.5×10^6 to 3.6×10^7 cells per cc.; the higher concentration naturally showed the lower rate per million cells. Under mass culture the one diatom species showed far greater variation in photosynthesis at different times, than did wild forms as widely separated as red and green algae. On the other hand, diatoms cultured in flasks under uniform conditions showed reasonably uniform behavior.

STUDIES IN SEDIMENTATION AND ON THE GEOLOGY OF THE CONTINENTAL SHELF

H. C. STETSON

In collaboration with Dr. J. A. Cushman, Miss Frances L. Parker and Dr. Fred B. Phleger, work on the sediments of the continental slope and of the nearby Atlantic Basin, as described in the last report is progressing satisfactorily; Dr. Phleger's report is finished and Dr. Cushman's and Miss Parker's is well advanced. My own section necessarily has to depend on the paleontological evidence supplied by the reports of the others and has just been started.

Through the kindness of Dr. A. C. Veatch his new charts of the continental slope, shortly to be published by the Geological Society of America, were made available for last summer's cruise. Cores were taken at topographically significant points in the canyons and on the slope from the Hudson Gorge to the latitude of Chesapeake Bay. The mechanical analyses have been completed.

The report on the sediments of the continental shelf was completed and published, and the chapter on the development of Oceanography, particularly along geological lines, was completed for the Geological Society of America's forthcoming anniversary volume. A short report was also prepared for a symposium on the Coastal Plain held at the Richmond meeting of the American Association for the Advancement of Science.

Dr. Maurice Ewing conducted further tests with his deep sea seismograph, and also experimented with an apparatus for retrieving instruments from the botton without a wire, the lifting force being supplied by oil-filled containers.

THE PRECIPITATION OF CALCIUM CARBONATE

KENNETH V. THIMANN

Experiments were made on the conditions governing the precipitation of $CaCO_3$ from waters, and the effect of the presence of excess $CaCO_3$ on the process, phenomena of importance for the understanding of the formation and dissolution of chalk banks, shells, etc.

Fresh sea water (Vineyard Sound) precipitates no $CaCO_3$ on standing, up to 15 days, but the addition of calcite causes a steady precipitation which reaches a maximum (at room temperature) of about 10 mg. per liter in 200 hours. Vigorous shaking has little effect on the rate of precipitation. Since the amounts of precipitate are so small, experiments were extended to distilled water saturated with calcium bicarbonate. This material precipitated $CaCO_3$ steadily on standing. Vigorous shaking hastens the precipitation but does not change the final value, which is reached in about ten days. The addition of calcite promotes the precipitation, but the same effect is exerted, though to a less extent, by powdered MnO_2 or by sugar charcoal. Thus the reaction is partially due to the provision of a large surface.

According to the literature, Woods Hole sea water should be strongly supersaturated with $CaCO_3$; on the other hand our data above show that precipitation is extremely slow, does not take place unless calcite is added, and in any event does not reach the expected values. This could be explained by the binding of the calcium carbonate by organic matter. Experiments on the addition of bacteria isolated from sea water on asparagine media, or of *b. coli* and some other organisms, showed no effect either on sea water or on the calcium bicarbonate solutions. Indeed, in several cases the precipitation was inhibited. The addition of gelatine or peptone at a concentration of 5 mgs. per liter, or of certain enzyme preparations, strongly inhibits the precipitation.

The tentative conclusion from these experiments is that small amounts of organic matter in some way interfere with the precipitation of $CaCO_3$, while even in the absence of organic matter solutions of calcium bicarbonate reach equilibrium only with extreme slowness.

LACTOSE-FERMENTING BACTERIA IN THE OCEAN

HAROLD A. THOMAS

The prevalence of lactose-fermenting bacteria in the ocean was studied, with particular regard to the determination of the proportion of these bacteria that would be indicative of human or land pollution. Of primary interest was the analysis of the value of simple lactose fermentation as an index of the intensity of pollution.

Fourteen stations in a line from New Bedford Harbor toward Robinson's Hole were sampled. The research was directed to determine (a) the number of samples containing lactose-fermenters; and (b) the number of lactose fermenting samples containing members of the coli-aerogenes group, indicating human or land pollution.

It was found that 29% of the water samples and 100% of the mud samples contained lactose-fermenting organisms. Of these samples only 54% contained members of the coli-aerogenes group of bacteria. Almost without exception the coli-aerogenes positive samples were obtained from stations located nearest to the pollution emanating from New Bedford Harbor.

The results show the presence of large numbers of bacteria in the ocean capable of fermenting lactose that bear no apparent relation to human or land pollution. Therefore, the Standard Presumptive test for intestinal bacteria, predicated upon the fermentation of lactose, is of little value as a criterion of pollution in salt water.

NITROGEN OF THE PARTICULATE MATTER IN THE SEA

THEODOR VON BRAND

Fourteen stations, all from the Montauk-Bermuda line, have been analyzed. The highest values were found at the shallow stations. The nitrogen values in the upper layers of the shelf stations were lower than these, but a little higher than those of the Sargasso Sea stations. In the deeper layers no significant difference could be found between these two latter localities. Distinct seasonal variations in the particulate nitrogen were seen only at the shallow localities, inshore.

STUDIES IN MARINE MICROBIOLOGY

SELMAN A. WAKSMAN, NORRIS W. RAKESTRAW, CORNELIA L. CAREY,
C. E. RENN, C. W. HOCK AND D. Q. ANDERSON

1. Chemical and Biological Oxidation of Organic Matter in the Sea Bottom and Associated Bacterial Processes—S. A. Waksman and D. Q. Anderson.

Previous studies of the oxidation of organic matter in marine bottoms have been continued. The new investigations concern the distribution and nature of organic matter in a large number of cores and bottom samples taken from sites near land, at distances from land in the Gulf of Maine, from the floor of the shelf, and from the deeps. The carbon and nitrogen contents of samples from various core profiles have been determined by chemical methods, and the oxygen consumptions of suspensions of mud incubated under controlled conditions applied as a biological method of measuring quantities of available organic matter in the same samples. The effect of immediate chemical absorption of oxygen by natural muds upon this procedure was also examined.

2. Occurrence of Nitrite and Nitrate Forming Bacteria in Sea Water—C. L. Carey.

Studies on the numbers and distribution of nitrifying bacteria in the sea, the work of several summers, were completed, and a summary of results published. Waters from various sources produce nitrite and nitrate at different rates; the processes go on more rapidly in muds than in water. Ammonia libration, nitrite formation, and nitrate production take place in a fixed sequence and at widely varying rates which are determined by the source of the water and mud and the nature and quantity of enriching materials used.

3. Decomposition of Chitin by Marine Bacteria—C. W. Hock.

The quantitative breakdown of Limulus chitin was studied in various natural media. In sea water alone the rate is immeasurable, but in mud and sand the chitin is readily attacked. A number of pure cultures of chitin-destroying bacteria were isolated from different sources. The morphology and growth characteristics of these organisms were determined.

4. Regeneration of Nitrogen from Decomposing Plankton—N. W. Rakestraw, C. E. Renn and Th. von Brand.

The changes in the various nitrogenous fractions assimilated by diatoms during growth, and those liberated by them on decomposition were studied by refined micro-methods in laboratory systems involving concentrations of pure strains of diatoms comparable to those found in the sea. Under these conditions plankton nitrogen is converted to inorganic nitrogen completely, and the various forms of the latter are reassimilated without loss to the system when the diatoms are permitted to grow. The several stages of nitrogen regeneration: organic nitrogen to ammonia to nitrite, and nitrite to nitrate, proceed in a fixed order and separately.

5. Regeneration of Nitrogen from Organic Matter of Marine Muds; Studies of Biological Oxygen demand, and Review of Literature of Marine Bacteriology—C. E. Renn.

The rate at which ammonia develops in stored mud indicates that inorganic nitrogen is regenerated from organic nitrogen in marine muds much more slowly than from plankton material. This low rate is determined by the biological stability of materials reaching the mud, by low temperatures and limited oxygen, and by decreased exchange with the overlying water. But it also appears that the inorganic constituents of the mud itself absorb bacteria and organic matter in such a way as to depress biological activity.

The amounts of oxygen consumed by biological activity in stored samples from stations in the Western Basin of the North Atlantic vary with the depth from which the samples are taken. More oxygen is consumed by superficial and by deep water than by water from the "intermediate oxygen-minimum" layer. Within limits this indicates a relatively small amount of biologically available material in the zone of the oxygen minimum concentrations.

A review of the work in marine bacteriology since 1925 is in preparation.

THE DISTRIBUTION OF VITAMINS A_1 AND A_2 IN FISHES

GEORGE WALD

The distribution of vitamins A_1 and A_2 has been determined in eye tissues and livers of a number of fishes. The eye tissues of all permanently fresh-water fishes examined contain vitamin A_2 alone. Those of all permanently marine fishes except the tautog contain only vitamin A_1. Those of all euryhaline (potentially migratory) fishes contain either predominantly or exclusively the vitamin A ordinarily associated with the environment in which the fish is spawned. The tautog is exceptional in possessing a typically anadromous vitamin A configuration, though it is a permanently marine fish.

These correlations extend in part to the liver oils, but most livers contain mixtures of both vitamins A, occasionally in proportions the reverse of those in the eye tissues.

MARINE BIOLOGY

TALBOT H. WATERMAN

During the summer of 1938 work was continued on the study of the bathyplankton, as well as on the taxonomy and comparative anatomy of the deep-sea angler-fishes (Ceratioidea), and experimental studies on the neuro-muscular mechanism in Crustacea were begun at the Bermuda Biological Station.

DIRECT MEASUREMENT OF CURRENTS

E. E. WATSON

The electrically recording current meter has been altered so as to remove most of the sources of trouble indicated by the preliminary trials in 1937, and the automatic recording apparatus for the meter was built, with the assistance of Mr. R. H. Hay. In August, the meter and recording apparatus were taken out on "Atlantis" for tests. After adjustments, the operation of both meter and recorder proved satisfactory, though a few minor improvements were indicated. At 250 meters, there was no indication of any trouble from pressure, and the design of the meter is such that it should function at any depth. For the electrical connection from meter to ship a 3/16 inch insulated cable was used. The meter was carried by the hydrographic cable and the electrical cable was lashed to this at intervals of about 30 meters or less. This method is not satisfactory for depths exceeding 200 meters. For deeper work it is planned to use a single insulated steel cable to support the meter and also to furnish the electrical circuit.

List of Contributions

LIST OF CONTRIBUTIONS

FROM THE WOODS HOLE OCEANOGRAPHIC INSTITUTION

No. 1. H. U. Sverdrup. Scientific Results of the *Nautilus* Expedition, 1931, under the Command of Captain Sir Hubert Wilkins. I. Introduction and Narrative. *Papers in Physical Oceanography and Meteorology*, Vol. II, No. 1, pp. 3–15. 1933.

No. 2. H. U. Sverdrup. Scientific Results of the *Nautilus* Expedition, 1931, under the Command of Captain Sir Hubert Wilkins. II. Oceanography. *Papers in Physical Oceanography and Meteorology*, Vol. II, No. 1, pp. 16–63. 1933.

No. 3. Floyd M. Soule. Scientific Results of the *Nautilus* Expedition, 1931, under the Command of Captain Sir Hubert Wilkins. III. Echo-Sounding. *Papers in Physical Oceanography and Meteorology*, Vol. II, No. 1, pp. 65-76. 1933.

No. 4. B. Villinger. Scientific Results of the *Nautilus* Expedition, 1931, under the Command of Captain Sir Hubert Wilkins. IV. Die Schweremessungen auf der *Nautilus* Expedition, 1931. *Papers in Physical Oceanography and Meteorology*, Vol. II, No. 3, pp. 3-16. 1933.

No. 5. Henry C. Stetson. Scientific Results of the *Nautilus* Expedition, 1931, under the Command of Captain Sir Hubert Wilkins. V. The Bottom Deposits. *Papers in Physical Oceanography and Meteorology*, Vol. II, No. 3, pp. 17-37. 1933.

No. 6. Selman A. Waksman and Cornelia L. Carey. Rôle of Bacteria in the Decomposition of Plant and Animal Residues in the Ocean. *Proc. Soc. Exper. Biol. and Med.*, Vol. XXX, pp. 526–527. 1933.

No. 7. Arda A. Green and Raymond W. Root. The Equilibrium between Hemoglobin and Oxygen in the Blood of certain Fishes. *Biol. Bull.*, Vol. LXIV, pp. 383-404. 1933.

No. 8. Norris W. Rakestraw. Studies on the Biology and Chemistry of the Gulf of Maine. I. Chemistry of the Waters of the Gulf of Maine in August, 1932. *Biol. Bull.*, Vol. LXIV, pp. 149-158. 1933.

No. 9. H. H. Gran. Studies on the Biology and Chemistry of the Gulf of Maine. II. Distribution of Phytoplankton in August, 1932. *Biol. Bull.*, Vol. LXIV, pp. 159-182. 1933.

No. 10. Selman A. Waksman, H. W. Reuszer, Cornelia L. Carey, Margaret Hotchkiss, and C. E. Renn. Studies on the Biology and Chemistry of the Gulf of Maine. III. Bacteriological Investigations of the Sea Water and Marine Bottoms. *Biol. Bull.* Vol. LXIV, pp. 183-205. 1933.

No. 11. Arda A. Green and Alfred C. Redfield. On the Respiratory Function of the Blood of the Porpoise. *Biol. Bull.* Vol. LXIV, pp. 44-52. 1933.

No. 12. Selman A. Waksman. On the Distribution of Organic Matter in the Sea Bottom and the Chemical Nature and Origin of Marine Humus. *Soil Sci.*, Vol. XXXVI, No. 2, pp. 125-147. 1933.

No. 13. A. C. Redfield. The Evolution of the Respiratory Function of the Blood. *Quart. Rev. Biol.*, Vol. VIII, No. 1, pp. 31-57. 1933.

No. 14. C. O'D. Iselin, II. Some Phases of Modern Deep-Sea Oceanography with a Description of some of the Equipment and Methods of the newly formed Woods Hole Oceanographic Institution. *Annual Report, Smithsonian Institution*, for year ending June 30, 1932, pp. 251-267. (Publication 3198.) 1933.

No. 15. E. Monroe Harwood and Charles F. Brooks. Monthly Sequence of Sea-Surface Temperature on the New York–San Juan Steamship Route. *Trans. Am. Geophys. Union, Fourteenth Annual Meeting*, pp. 173-180. 1933.

No. 16. Alfred C. Redfield and Elizabeth N. Ingalls. The Oxygen Dissociation Curves of some Bloods containing Hemocyanin. *Jour. Cell. and Comp. Physiol.*, Vol. III, No. 2, pp. 169-202. 1933.

No. 17. Selman A. Waksman, Cornelia L. Carey, and Herbert W. Reuszer. Marine Bacteria and their Rôle in the Cycle of Life in the Sea. I. Decomposition of Marine Plant and Animal Residues by Bacteria. *Biol. Bull.*, Vol. LXV, pp. 57-78. 1933.

No. 18. Selman A. Waksman, Margaret Hotchkiss, and Cornelia L. Carey. Marine Bacteria and their Rôle in the Cycle of Life in the Sea. II. Bacteria concerned in the Cycle of Nitrogen in the Sea. *Biol. Bull.*, Vol. LXV, pp. 137-167. 1933.

No. 19. Herbert W. Reuszer. Marine Bacteria and their Rôle in the Cycle of Life in the Sea. III. The Distribution of Bacteria in the Ocean Waters and Muds about Cape Cod. *Biol. Bull.*, Vol. LXV, pp. 480-497. 1933.

No. 20. John Colman. The Woods Hole Oceanographic Institution: Sonic Soundings, and an Account of a Winter Cruise to the Somers Islands. *The Geographical Journal*, Vol. LXXXII, pp. 326-336. 1933.

No. 21. John H. Welsh. Light Intensity and the Extent of Activity of Locomotor Muscles as Opposed to Cilia. *Biol. Bull.*, Vol. LXV, pp. 168-174. 1933.

No. 22. Alfred C. Redfield. The Haemocyanins. *Biol. Rev.*, Vol. IX, No. 2, pp. 175-212. 1934.

No. 23. Selman A. Waksman. The Rôle of Bacteria in the Cycle of Life in the Sea. *Scientific Monthly*. Vol. XXXVIII, pp. 35-49. 1934.

No. 24. H. R. Seiwell. The Annual Organic Production and Nutrient Phosphorus Requirement in the Tropical Western North Atlantic. *Jour. d. Conseil*, Vol. X, No. 1, pp. 20-32. 1935.

No. 25. H. R. Seiwell and G. E. Seiwell. Über den Gesamtphosphorgehalt des Seewassers im westlichen Nordatlantischen Ozean. *Annalen der Hydrographie und Maritimen Meteorologie*, Vol. LXII, pp. 7-13. 1934.

No. 26. George L. Clarke. Observations on the Penetration of Daylight into Mid-Atlantic and Coastal Waters. *Biol. Bull.*, Vol. LXV, pp. 317-337. 1933.

No. 27. C. O'D. Iselin. The Development of our Conception of the Gulf Stream. *Trans. Am. Geophys. Union, Fourteenth Annual Meeting*, pp. 226-231. 1933.

No. 28. August Krogh. A Method for the Determination of Ammonia in Water and Air. *Biol. Bull.*, Vol. LXVII, pp. 126-131. 1934.

No. 29. Norris W. Rakestraw and Frank B. Lutz. Arsenic in Sea Water. *Biol. Bull.*, Vol. LXV, pp. 397-401. 1933.

No. 30. Alfred C. Redfield. On the Proportions of Organic Derivatives in Sea Water and their Relation to the Composition of Plankton. *James Johnstone Memorial Volume, University of Liverpool*, pp. 176-192. 1934.

No. 31. Philip H. Mitchell and Norris W. Rakestraw. The Buffer Capacity of Sea Water. *Biol. Bull.*, Vol. LXV, pp. 437-450. 1933.

No. 32. H. R. Seiwell. The Distribution of Oxygen in the Western Basin of the North Atlantic. *Papers in Physical Oceanography and Meteorology*, Vol. III, No. 1, 86 pp. 1934.

No. 33. George L. Clarke. Diurnal Migration of Plankton in the Gulf of Maine and its Correlation with Changes in Submarine Irradiation. *Biol. Bull.*, Vol. LXV, pp. 402-435. 1933.

No. 34. Henry B. Bigelow. Studies of the Waters on the Continental Shelf, Cape Cod to Chesapeake Bay. I. The Cycle of Temperature. *Papers in Physical Oceanography and Meteorology*, Vol. II, No. 4, 135 pp. 1933.

No. 35. Albert Eide Parr. Report on Experimental Use of a Triangular Trawl for Bathypelagic Collecting. *Bull. Bingham Oceanographic Coll.*, Vol. IV, Art. 6, pp. 1-59. 1934.

No. 36. G. H. Parker and Helen Porter. The control of the Dermal Melanophores in Elasmobranch Fishes. *Biol. Bull.*, Vol. LXVI, pp. 30-37. 1934.

No. 37. G. H. Parker. The Color Changes of Elasmobranch Fishes. *Proc. Nat. Acad. Sci.*, Vol. 19, pp. 1038-1039. 1933.

No. 38. Raymond W. Root. The Combination of Carbon Monoxide with Hemocyanin. *Jour. Biol. Chem.*, Vol. 104, No. 2, pp. 239-244. 1934.

No. 39. Selman A. Waksman. The Distribution and Conditions of Existence of Bacteria in the Sea. *Ecological Monographs*, Vol. 4, No. 4, pp. 523-529. 1934.

No. 40. G. L. Clarke. The Rôle of Copepods in the Economy of the Sea. *Fifth Pacific Science Congress*, Vancouver, B. C., a 5.5, pp. 2017-2021. 1934.

No. 41. George L. Clarke. Factors Affecting the Vertical Distribution of Copepods. *Ecological Monographs*, Vol. 4, No. 4, pp. 530-540. 1934.

No. 42. Philip H. Mitchell and Julian L. Solinger. The Effects of Land Drainage upon the Excess Bases of Sea Water. *Biol. Bull.*, Vol. LXVI, No. 2, pp. 97-101. 1934.

No. 43. Selman A. Waksman, Cornelia L. Carey and Melvin C. Allen. Bacteria Decomposing Alginic Acid. *Jour. Bacteriology*, Vol. 28, No. 2, pp. 213-220. 1934.

No. 44. Cornelia L. Carey and Selman A. Waksman. The Presence of Nitrifying Bacteria in Deep Seas. *Science*, Vol. 79, No. 2050, pp. 349-350. 1934.

No. 45. G. L. Clarke and R. H. Oster. The Penetration of the Blue and Red Components of Daylight into Atlantic Coastal Waters and its Relation to Phytoplankton Metabolism. *Biol. Bull.*, Vol. LXVII, No. 1, pp. 59-75. 1934.

No. 46. Trygve Braarud. A Note on the Phytoplankton of the Gulf of Maine in the Summer of 1933. *Biol. Bull.*, Vol. LXVII, No. 1, pp. 76-82. 1934.

No. 47. August Krogh and Ancel Keys. Methods for the Determination of Dissolved Organic Carbon and Nitrogen in Sea Water. *Biol. Bull.*, Vol. LXVII, No. 1, pp. 132-144. 1934.

No. 48. George L. Clarke. Further Observations on the Diurnal Migration of Copepods in the Gulf of Maine. *Biol. Bull.*, Vol. LXVII, No. 3, pp. 432-455. 1934.

No. 49. Phil E. Church. Surface-Temperatures on the New York to Cape São Roque Steamship-Route. *Trans. Am. Geophys. Union, Fifteenth Annual Meeting*, pp. 204-208. 1934.

No. 50. Raymond W. Root and Arda Alden Green. The Effect of Acidity on the Carbon Monoxide-Combining Power of Hemoglobin in the Blood of Marine Fishes. *Jour. Biol. Chem.*, Vol. 106, No 2, pp. 545-552. 1934.

No. 51. C. O'D. Iselin. Temperature-Salinity Correlation within the Florida Current. *Trans. Am. Geophys. Union, Fifteenth Annual Meeting*, pp. 208-209. 1934.

No. 52. H. C. Stetson and Marshall Schalk. Marine Erosion of Glacial Deposits in Massachusetts Bay. *Jour. Sedimentary Petrology*, Vol. 5, No. 1, pp. 40-51. 1935.

No. 53. Charles E. Renn. Wasting Disease of Zostera in American Waters. *Nature*, Vol. 134, p. 416. 1934.

No. 54. George L. Clarke. The Diurnal Migration of Copepods in St. Georges Harbor, Bermuda. *Biol. Bull.*, Vol. LXVII, No. 3, pp. 456-460. 1934.

No. 55. F. A. Brown, Jr. The Chemical Nature of the Pigments and the Transformations Responsible for Color Changes in Palaemonetes. *Biol. Bull.*, Vol LXVII, No. 3, pp. 365-380. 1934.

No. 56. R. M. Bond. Digestive Enzymes of the Pelagic Copepod, *Calanus finmarchicus*. *Biol. Bull.*, Vol. LXVII, No. 3, pp. 461-465. 1934.

No. 57. Selman A. Waksman and Cornelia L. Carey. Decomposition of Organic Matter in Sea Water by Bacteria. I. Bacterial Multiplication in Stored Sea Water. *Jour. Bacteriology*, Vol. 29, No. 5, pp. 531-543. 1935.

No. 58. R. H. Oster and G. L. Clarke. The Penetration of the Red, Green and Violet Components of Daylight into Atlantic Waters. *Jour. Optical Soc. Amer.*, Vol. 25, No. 3, pp. 1-16. 1935.

No. 59. Benjamin B. Leavitt. A Quantitative Study of the Vertical Distribution of the Larger Zoöplankton in Deep Water. *Biol. Bull.*, Vol. LXVIII, No. 1, pp. 115-130. 1935.

No. 60. G. H. Parker. The Electric Stimulation of Chromatophoral Nerve-Fibers in the Dogfish. *Biol. Bull.*, Vol. LXVIII, No. 1, pp. 1-3. 1935.

No. 61. Henry B. Bigelow and W. C. Schroeder. Canadian Atlantic Fauna. 12. Chordata; 12d. Marsipobranchii (Lampreys); 12e. Elasmobranchii (Sharks and Rays); 12f. Holocephali (Chimaeroids). *Biological Board of Canada*. pp. 1-38. 1934.

No. 62. In preparation.

No. 63. Gladys Eddy Seiwell. Note on Iron Analyses of Atlantic Coastal Waters. *Ecology*, Vol. XVI, No. 4, pp. 663-664. 1935.

No. 64. H. R. Seiwell. The Phosphorus Cycle in the Western Basin of the North Atlantic. Part I. The Distribution of Phosphate and Organic Phosphorus. *Papers in Physical Oceanography and Meteorology*, Vol. 3, No. 4, pp. 1-56. 1935.

No. 65. James B. Lackey. Occurrence and Distribution of the Marine Protozoan Species in the Woods Hole Area. *Biol. Bull.*, Vol. LXX, No. 2, pp. 264–278. 1936.

No. 66. G. L. Clarke and S. S. Gellis. The Nutrition of Copepods in Relation to the Food-Cycle of the Sea. *Biol. Bull.*, Vol. LXVIII, No. 2, pp. 231-246. 1935.

No. 67. Charles E. Renn. A Mycetozoan Parasite of *Zostera marina*. *Nature*. Vol. 135, p. 544. 1935.

No. 68. Selman A. Waksman and Cornelia L. Carey. Decomposition of Organic Matter in Sea Water by Bacteria. II. Influence of Addition of Organic Substances upon Bacterial Activities. *Jour. Bacteriology*, Vol. 29, No. 5, pp. 545-561. 1935.

No. 69. H. H. Gran and Trygve Braarud. A Quantitative Study of the Phytoplankton in the Bay of Fundy and the Gulf of Maine (including Observations on Hydrography, Chemistry and Turbidity). *Jour. Biol. Bd. Canada*, Vol. 1, No. 5, pp. 279-467. 1935.

No. 70. Henry B. Bigelow and Mary Sears. Studies on the Waters of the Continental Shelf, Cape Cod to Chesapeake Bay. II. Salinity. *Papers in Physical Oceanography and Meteorology*, Vol. 4, No. 1, pp. 1-94. 1935.

No. 71. C. G. Rossby and R. B. Montgomery. The Layer of Frictional Influence in Wind and Ocean Currents. *Papers in Physical Oceanography and Meteorology*, Vol. 3, No. 3, pp. 1-101. 1935.

No. 72. In preparation.

No. 73. F. K. Sparrow, Jr. The Occurrence of Saprophytic Fungi in Marine Muds. *Biol. Bull.*, Vol. LXXIII, No. 2, pp. 242-248. 1937.

No. 74. Philip H. Mitchell and Ivon R. Taylor. The Dissociation Constant of Cresol Red in Sea Water. *Jour. d. Conseil*, Vol. 10, No. 2, pp. 169-172. 1935.

No. 75. L. Irving, D. Y. Solandt and O. M. Solandt. Nerve Impulses from Branchial Pressure Receptors in the Dogfish. *Jour. Physiol.* Vol. 84, No. 2, p. 187. 1935.

No. 76. H. C. Stetson. Bed-Rock from the Continental Margin on Georges Bank. *Trans. Am. Geophys. Union, Sixteenth Annual Meeting*, pp. 226-228. 1935.

No. 77. H. R. Seiwell. Phosphate in the Western Basin of the North Atlantic. *Nature*, Vol. 136, p. 206. 1935.

No. 78. Selman A. Waksman and Charles E. Renn. Decomposition of Organic Matter in Sea Water by Bacteria. III. Factors Influencing the Rate of Decomposition. *Biol. Bull.*, Vol. LXX, No. 3, pp. 472–483. 1936.

No. 79. Ancel Keys, E. H. Christensen, and August Krogh. The Organic Metabolism of Sea-water with Special Reference to the Ultimate Food Cycle in the Sea. *Jour. Marine Biol. Assoc.*, Vol. XX, No. 2, pp. 181-196. 1935.

No. 80. Henry C. Stetson. Geology and Paleontology of the Georges Bank Canyons. I. Geology. *Bull. Geol. Soc. Amer.*, Vol. 47, pp. 339–366. 1936.

No. 81. Lloyd William Stephenson. Geology and Paleontology of the Georges Bank Canyons. II. Upper Cretaceous Fossils from Georges Bank (including Species from Banquereau, Nova Scotia). *Bull. Geol. Soc. Amer.*, Vol. 47, pp. 367–410. 1936.

No. 82. Joseph A. Cushman. Geology and Paleontology of the Georges Bank Canyons. IV. Cretaceous and Late Tertiary Foraminifera. *Bull. Geol. Soc. Amer.*, Vol. 47, pp. 413–440. 1936.

No. 83. George Wald. Pigments of the Retina. II. Sea Robin, Sea Bass, and Scup. *Jour. Gen. Physiol.*, Vol. 20, No. 1, pp. 45–56. 1936.

No. 84. R. S. Bassler. Geology and Paleontology of the Georges Bank Canyons. III. Cretaceous Bryozoan from Georges Bank. *Bull. Geol. Soc. Amer.*, Vol. 47, pp. 411–412. 1936.

No. 85. Charles J. Fish. The Biology of *Calanus finmarchicus* in the Gulf of Maine and Bay of Fundy. *Biol. Bull.* Vol. LXX, No. 1, pp. 118–141. 1936.

No. 86. Norris W. Rakestraw, Henry E. Mahncke and Eliot F. Beach. Determination of Iron in Sea Water. *Analytical edition Ind. and Eng. Chem.*, Vol. 8, pp. 136–138. 1936.

No. 87. Norris W. Rakestraw and Henry E. Mahncke. Boron Content of Sea Water of the North Atlantic Coast. *Analytical edition Ind. and Eng. Chem.*, Vol. 7, p. 425. 1935.

No. 88. E. E. Watson. Mixing and Residual Currents in Tidal Waters as Illustrated in the Bay of Fundy. *Jour. Biol. Bd. Canada*, 2 (2), pp. 141–208. 1936.

No. 89. George Wald. The Visual Purple System in Marine Fishes. *Nature*, Vol. 136, p. 913. 1935.

No. 90. Charles E. Renn. The Wasting Disease of *Zostera marina*. I. A Phytological Investigation of the Diseased Plant. *Biol. Bull.*, Vol. LXX, No. 1, pp. 148–158. 1936.

No. 91. S. Edward Roos. Some Geographical Results of the Second Byrd Antarctic Expedition, 1933-1935. I. The Submarine Topography of the Ross Sea and Adjacent Waters. *Geog. Rev.*, Vol. XXVII, No. 4, pp. 574-583. 1937.

No. 92. John L. Fuller and George L. Clarke. Further Experiments on the Feeding of *Calanus finmarchicus*. *Biol. Bull.*, Vol. LXX, No. 2, pp. 308-320. 1936.

No. 93. Maurice Ewing, A. P. Crary, and H. M. Rutherford. Geophysical Investigations in the Emerged and Submerged Atlantic Coastal Plain. I. Methods and Results. *Bull. Geol. Soc. Amer.*, Vol. 48, pp. 753-802. 1937.

No. 94. Charles J. Fish. The Biology of *Pseudocalanus minutus* in the Gulf of Maine and Bay of Fundy. *Biol. Bull.*, Vol. LXX, No. 2, pp. 193–216. 1936.

No. 95. Frank H. Johnson. The Oxygen Uptake of Marine Bacteria. *Jour. Bacteriology*, Vol. 31, No. 5, pp. 547–556. 1936.

No. 96. Michael Graham. Investigations of the Herring of Passamaquoddy and Adjacent Regions. *Jour. Biol. Bd. Canada*, 2 (2), pp. 95–140. 1936.

No. 97. A. E. Parr. On the Probable Relationship Between Vertical Stability and Lateral Mixing Processes. *Jour. d. Conseil*, Vol. XI, No. 3, pp. 299–313. 1936.

No. 98. Wilson M. Powell and George L. Clarke. The Reflection and Absorption of Daylight at the Surface of the Ocean. *Jour. Optical Soc. Amer.*, Vol. 26, pp. 1–23. 1936.

No. 99. F. K. Sparrow, Jr. Biological Observations on the Marine Fungi of Woods Hole Waters. *Biol. Bull.*, Vol. LXX, No. 2, pp. 236–263. 1936.

No. 100. George L. Clarke. On the Depth at which Fish Can See. *Ecology*, Vol. 17, No. 3, pp. 452–456. 1936.

No. 101. George L. Clarke. Light Penetration in the Western North Atlantic and its Application to Biological Problems. *Rapp. et Proc. Verb. Cons. Perm. Internat. Exp. Mer.*, Vol. 101, Pt. 2, pp. 1–14. 1936.

No. 102. C.-G. Rossby and R. B. Montgomery. I. On the Frictional Force between Air and Water and on the Occurrence of a Laminar Boundary Layer next to the Surface of the Sea. C.-G. Rossby. II. Measurements of Vertical Gradient of Wind over Water. R. B. Montgomery. III. Transport of Surface Water due to the Wind System over the North Atlantic. R. B. Montgomery. *Papers In Physical Oceanography and Meteorology*, Vol. 4, No. 3, pp. 1–101. 1936.

No. 103. H. C. Stetson. Dredge-Samples from the Submarine Canyons between the Hudson Gorge and Chesapeake Bay. *Trans. Am. Geophys. Union*, *Seventeenth Annual Meeting*, pp. 223–225. 1936.

No. 104. Columbus Iselin. The Influence of the Mediterranean Outflow at Mid-Depths in the Sargasso Sea. *Trans. Am. Geophys. Union*, *Seventeenth Annual Meeting*, pp. 219–221. 1936.

No. 105. R. B. Montgomery. Computation of the Transport of Surface-Water due to the Wind-System over the North Atlantic. *Trans. Am. Geophys. Union*, *Seventeenth Annual Meeting*, pp. 225–229. 1936.

No. 106. Margaret Hotchkiss and Selman A. Waksman. Correlative Studies of Microscopic and Plate Methods for Evaluating the Bacterial Population of the Sea. *Jour. Bacteriology*, Vol. 32, No. 4, pp. 423–432. 1936.

No. 107. Edward H. Smith, Floyd M. Soule, Olav Mosby. The "Marion" and "General Greene" Expeditions to Davis Strait and Labrador Sea under Direction of the United States Coast Guard 1928-1931-1933-1934-1935. Scientific Results. Part 2. Physical Oceanography. *U. S. Coast Guard Bull.*, No. 19, pp. I-VI, pp. 1–259. 1937.

No. 108. Columbus Iselin. Study of the Circulation of the North Atlantic Ocean. *Papers in Physical Oceanography and Meteorology*, Vol. 4, No. 4, pp. 1-101. 1936.

No. 109. Charles J. Fish. The Biology of *Oithona similis* in the Gulf of Maine and Bay of Fundy. *Biol. Bull.*, Vol. LXXI, No. 1, pp. 168–187. 1936.

No. 110. Norris W. Rakestraw. The Occurrence and Significance of Nitrite in the Sea. *Biol. Bull.*, Vol. LXXI, No. 1, pp. 133–167. 1936.

No. 111. Charles E. Renn. The Eel-Grass Situation along the Middle Atlantic Coast. *Ecology*, Vol. 18, No. 2, pp. 323-325. 1937.

No. 112. George L. Clarke and Donald J. Zinn. Seasonal Production of Zoöplankton off Woods Hole with Special Reference to *Calanus finmarchicus*. *Biol. Bull.*, Vol. LXXIII, No. 3, pp. 464–487. 1937.

No. 113. G. H. Parker. The Reactivation by Cutting of Severed Melanophore Nerves in the Dogfish Mustelus. *Biol. Bull.*, Vol. LXXI, No. 2, pp. 255–258. 1936.

No. 114. Philip H. Mitchell, Kurt Buch and Norris W. Rakestraw. The Effect of Salinity and Temperature upon the Dissociation of Cresol Red and Phenol Red in Sea Water. *Jour. d. Conseil*, Vol. XI, No. 2, pp. 183–189. 1936.

No. 115. C.-G. Rossby. Dynamics of Steady Ocean Currents in the Light of Experimental Fluid Mechanics. *Papers in Physical Oceanography and Meteorology*, Vol. 5, No. 1, pp. 1–43. 1936.

No. 116. Charles P. Winsor and Lionel A. Walford. Sampling Variations in the Use of Plankton Nets. *Jour. d. Conseil*, Vol. XI, No. 2, pp. 190–204. 1936.

No. 117. Charles E. Renn. Persistence of the Eel-Grass Disease and Parasite on the American Atlantic Coast. *Nature*, Vol. 138, p. 507. 1936.

No. 118. H. R. Seiwell. Relationship of Minimum Oxygen Concentration to Density of the Water Column in the Western North Atlantic. *Gerlands Beiträge zur Geophysik*, Vol. 50, pp. 302–306. 1937.

No. 119. Henry B. Bigelow and William C. Schroeder. Supplemental Notes on Fishes of the Gulf of Maine. *Bull. Bur. Fisheries*, Vol. XLVIII, Bull. No. 20, pp. 319–343. 1936.

No. 120. Norris W. Rakestraw and Alexander Hollaender. Photochemical Oxidation of Ammonia in Sea Water. *Science*, Vol. 84, No. 2185, pp. 442–443. 1936.

No. 121. Phil E. Church. Temperatures of the Western North Atlantic from Thermograph Records. *Publ. Scientifique*, No. 4, pp. 1–32. 1937.

No. 122. Alfred C. Redfield. An Ecological Aspect of the Gulf Stream. *Nature*, Vol. 138, p. 1013. 1936.

No. 123. Theodor von Brand. Observations upon the Nitrogen of the Particulate Matter in the Sea. *Biol. Bull.*, Vol. LXXII, No. 1, pp. 1–6. 1937.

No. 124. Selman A. Waksman and Margaret Hotchkiss. Viability of Bacteria in Sea Water. *Jour. Bacteriol.*, Vol. 33, No. 4, pp. 389–400. 1937.

No. 125. Albert Eide Parr. A Contribution to the Hydrography of the Caribbean and Cayman Seas. Based upon the observations made by the Research Ship "Atlantis", 1933–34. *Bull. Bingham Oceanographic Coll.*, Vol. V, Art. 4, pp. 1–110. 1937.

No. 126. J. H. Welsh and F. A. Chace, Jr. Eyes of Deep Sea Crustaceans. I. Acanthephyridae *Biol. Bull.*, Vol. LXXII, No. 1, pp. 57–74. 1937.

No. 127. Alfred C. Redfield, Homer P. Smith and Bostwick Ketchum. The Cycle of Organic Phosphorus in the Gulf of Maine. *Biol. Bull.*, Vol. LXXIII, No. 3, pp. 421–443. 1937.

No. 128. William F. Wrath. Contamination and Compaction on Core Sampling. *Science*, Vol. 84, No. 1289, pp. 537–538. 1936.

No. 129. Theodor von Brand, Norris W. Rakestraw and Charles E. Renn. The Experimental Decomposition and Regeneration of Nitrogenous Organic Matter in Sea Water. *Biol. Bull.*, Vol. LXXII, No. 2, pp. 165-175. 1937.

No. 130. H. C. Stetson and J. E. Upson. Bottom Deposits of the Ross Sea. *Jour. Sedimentary Petrology*, Vol. 7, No. 2, pp. 55–66. 1937.

No. 131. G. H. PARKER. Integumentary Color Changes of Elasmobranch Fishes Especially of Mustelus. *Proc. Am. Philos. Soc.*, Vol. 77, No. 3, pp. 223–247. 1937.

No. 132. JOHN L. FULLER. Feeding Rate of *Calanus finmarchicus* in Relation to Environmental Conditions. *Biol. Bull.*, Vol. LXXII, No. 2, pp. 233–246. 1937.

No. 133. CHARLES E. RENN. Bacteria and the Phosphorus Cycle in the Sea. *Biol. Bull.*, Vol. LXXII, No. 2, pp. 190–195. 1937.

No. 134. ROBERT C. STAUFFER. Changes in the Invertebrate Community of a Lagoon after Disappearance of the Eel Grass. *Ecology*, Vol. 18, No. 3, pp. 427–431. 1937.

No. 135. CHARLES J. FISH and MARTIN W. JOHNSON. The Biology of the Zoöplankton Population in the Bay of Fundy and Gulf of Maine with Special Reference to Production and Distribution. *J. Biol. Bd. Can.*, Vol. 3, No. 3, pp. 189–322. 1937.

No. 136. MARSHALL SCHALK. A Textural Study of the Outer Beach of Cape Cod, Massachusetts. *Jour. Sedimentary Petrology*, Vol. 8, No. 2, pp. 41-54. 1938.

No. 137. H. R. SEIWELL. Short Period Vertical Oscillations in the Western Basin of the North Atlantic. *Papers in Physical Oceanography and Meteorology*, Vol. V, No. 2, pp. 1–44. 1937.

No. 138. H. R. SEIWELL. The Minimum Oxygen Concentration in the Western Basin of the North Atlantic. *Papers in Physical Oceanography and Meteorology*, Vol. V, No. 3, pp. 1–24. 1937.

No. 139. H. R. SEIWELL. The Oxygen-Poor Layer in the Western North Atlantic. *Jour. d. Conseil*, Vol. XII, No. 3, pp. 277–283. 1937.

No. 140. NORRIS W. RAKESTRAW and HOMER P. SMITH. A Contribution to the Chemistry of the Caribbean and Cayman Seas. *Bull. Bingham Oceanographic Coll.*, Vol. VI, Art. 1, pp. 1–41. 1937.

No. 141. NORRIS W. RAKESTRAW and VICTOR M. EMMEL. The Determination of Dissolved Nitrogen in Water. *Analytical edition Ind. and Eng. Chem.*, Vol. 9, pp. 1–6. 1937.

No. 142. H. R. SEIWELL. Short-Period Variations of Oceanographic Characteristics in the Western North Atlantic. *Trans. Am. Geophys. Union, Eighteenth Annual Meeting*, pp. 220–222. 1937.

No. 143. H. C. STETSON. Current-Measurements in the Georges Bank Canyons. *Trans. Am. Geophys. Union, Eighteenth Annual Meeting*, pp. 216–219. 1937.

No. 144. MARGARET RUTH BUTLER. The Effect of its Nitrogen Content on the Decomposition of the Polysaccharide Extract of *Chondrus crispus*. *Biol. Bull.*, Vol. LXXIII, No. 1, pp. 143–146. 1937.

No. 145. J. H. WELSH, F. A. CHACE, JR., and R. F. NUNNEMACHER. The Diurnal Migration of Deep-Water Animals. *Biol. Bull.*, Vol. LXXIII, No. 2, pp. 185-196. 1937.

No. 146. H. C. STETSON and J. FRED SMITH. Behavior of Suspension Currents and Mud Slides on the Continental Slope. *Am. Jour. Sc.*, *Fifth Series*, Vol. XXXV, No. 205, pp. 1–13. 1937.

No. 147. HENRY B. BIGELOW. Plankton of the Bermuda Oceanographic Expeditions. VIII. Medusae taken during the Years 1929 and 1930. *Zoological*, Vol. XXIII, No. 5, pp. 99-189. 1938.

No. 148. Abby H. Turner. Serum Protein Measurements in the Lower Vertebrates. II. In Marine Teleosts and Elasmobranchs. *Biol. Bull.*, Vol. LXXIII, No. 3, pp. 511–526. 1937.

No. 149. Albert Eide Parr. On the Longitudinal Variations in the Dynamic Elevation of the Surface of the Caribbean Current. *Bull. Bingham Oceanographic Coll.*, Vol. VI, Art. 2, pp. 1–20. 1937.

No. 150. Gordon A. Riley. The Significance of the Mississippi River Drainage for Biological Conditions in the Northern Gulf of Mexico. *Sears Found. Jour. Mar. Res.*, Vol. I, No. 1, pp. 60–74. 1937.

No. 151. H. R. Seiwell. Consumption of Oxygen in Sea Water under Controlled Laboratory Conditions. *Nature*, Vol. 140, p. 506. 1937.

No. 152. H. R. Seiwell and Gladys Eddy Seiwell. The Sinking of Decomposing Plankton in Sea Water and its Relationship to Oxygen Consumption and Phosphorus Liberation. *Proc. Am. Philos. Soc.*, Vol. 78, No. 3, pp. 465–481. 1938.

No. 153. R. B. Montgomery. A Suggested Method for Representing Gradient Flow in Isentropic Surfaces. *Bull. Am. Meteorol. Soc.*, Vol. 18, pp. 210–212. 1937.

No. 154. Floyd M. Soule. Oceanography. Excerpt from International Ice Observation and Ice Patrol Service in the North Atlantic Ocean, Season of 1936. *U. S. Coast Guard Bull.*, No. 26, pp. 33-82. 1938.

No. 155. Albert Eide Parr. Report on Hydrographic Observations at a Series of Anchor Stations across the Straits of Florida. *Bull. Bingham Oceanographic Coll.*, Vol. VI, Art. 3, pp. 1–62. 1937.

No. 156. Lois C. Lillick. Seasonal Studies of the Phytoplankton off Woods Hole, Massachusetts. *Biol. Bull.*, Vol. LXXIII, No. 3, pp. 488–503. 1937.

No. 157. Selman A. Waksman, J. L. Stokes and Margaret R. Butler. Relation of Bacteria to Diatoms in Sea Water. *Jour. Mar. Biol. Assoc.*, Vol. XXII, pp. 359–373. 1937.

No. 158. Athelstan F. Spilhaus. Note on the Flow of Streams in a Rotating System. *Sears Found. Jour. Mar. Res.*, Vol. I, No. 1, pp. 29–33. 1937.

No. 159. Alfred C. Redfield and Ancel B. Keys. The Distribution of Ammonia in the Waters of the Gulf of Maine. *Biol. Bull.*, Vol. LXXIV, No. 1, pp. 83–92. 1938.

No. 160. Selman A. Waksman, Margaret Hotchkiss, Cornelia L. Carey and Y. Hardman. Decomposition of Nitrogenous Substances in Sea Water by Bacteria. *Jour. Bacteriology*, Vol. 35, No. 5, pp. 477-486. 1938.

No. 161. Selman A. Waksman and Unto Vartiovaara. The Absorption of Bacteria by Marine Bottom. *Biol. Bull.* Vol. LXXIV, No. 1, pp. 56–63. 1938.

No. 162. H. R. Seiwell. Application of the Distribution of Oxygen to the Physical Oceanography of the Caribbean Sea Region. *Papers in Physical Oceanography and Meteorology*, Vol. VI, No. 1, pp. 1-60. 1938.

No. 163. Theodor von Brand. Quantitative Determination of the Nitrogen in the Particulate Matter of the Sea. *Jour. d. Conseil*, Vol. XII, No. 2, pp. 187-196. 1938.

No. 164. George L. Clarke. On Securing Large Quantities of Diatoms from the Sea for Chemical Analysis. *Science*, Vol. 86, No. 2243, pp. 593–594. 1937.

No. 165. Selman A. Waksman and Margaret Hotchkiss. On the Oxidation of Organic Matter in Marine Sediments by Bacteria. *Sears Found. Jour. Mar. Res.*, Vol. I, No. 2, pp. 101-118. 1938.

No. 166. George L. Clarke. Seasonal Changes in the Intensity of Submarine Illumination off Woods Hole. *Ecology*, Vol. 19, No. 1, pp. 89–106. 1938.

No. 167. Athelstan F. Spilhaus. A Bathythermograph. *Sears Found. Jour. Mar. Res.*, Vol. I, No. 2, pp. 95-100. 1938.

No. 168. George L. Clarke. Light Penetration in the Caribbean Sea and in the Gulf of Mexico. *Sears Found. Jour. Mar. Res.*, Vol. I, No. 2, pp. 85-94. 1938.

No. 169. H. C. Stetson. Present Status of the Problem of Submarine Canyons. *Proc. Amer. Philos. Soc.*, Vol. 79, No. 1, pp. 27-33. 1938.

No. 170. R. B. Montgomery. Fluctuations in Monthly Sea Level on Eastern U. S. Coast as Related to Dynamics of Western North Atlantic Ocean. *Sears Found. Jour. Mar. Res.*, Vol. I, No. 2, pp. 165-185. 1938.

No. 171. C. O'D. Iselin. The influence of Fluctuations in the Major Ocean Current on the Climate and the Fisheries. *The Collecting Net*, Vol. XIII, No. 7, pp. 1-4. 1938.

No. 172. Bostwick H. Ketchum and Alfred C. Redfield. A Method for Maintaining a Continuous Supply of Marine Diatoms by Culture. *Biol. Bull.* Vol. LXXV, No. 1, pp. 165-169. 1938.

No. 173. Floyd M. Soule. Oceanography. Excerpt from International Ice Observation and Ice Patrol Service in the North Atlantic Ocean, Season of 1937. *U. S. Coast Guard Bull.*, No. 27, pp. 71–126. 1938.

No. 174. Benjamin B. Leavitt. The Quantitative Vertical Distribution of Macrozoöplankton in the Atlantic Ocean Basin. *Biol. Bull.*, Vol. LXXIV, No. 3, pp. 376-394. 1938.

No. 175. Norris W. Rakestraw and Victor M. Emmel. The Solubility of Nitrogen and Argon in Sea Water. *Jour. Phys. Chem.*, Vol. 42, No. 9, pp. 1211-1215. 1938.

No. 176. J. H. Welsh and F. A. Chace, Jr. Eyes of Deep-Sea Crustaceans II. Sergestidae. *Biol. Bull.*, Vol. LXXIV, No. 3, pp. 364-375. 1938.

No. 177. H. R. Seiwell. Eddy Diffusion at Mid-Depths in the Carribbean Sea Region. *Jour. d. Conseil.*, Vol. XIII, No. 2, pp. 155-162. 1938.

No. 178. H. C. Stetson. The Sediments of the Continental Shelf off the Eastern Coast of the United States. *Papers in Physical Oceanography and Meteorology*, Vol. V, No. 4, pp. 1-48. 1938.

No. 179. Albert Eide Parr. Further Observations on the Hydrography of the Eastern Caribbean and Adjacent Atlantic Waters. *Bull. Bingham Oceanographic Coll.*, Vol. 6, Art. 4, pp. 1-29. 1938.

No. 180. C. O'D. Iselin. A Promising Theory Concerning the Causes and Results of Long-Period Variations in the Strength of the Gulf Stream System. *Trans. Am. Geophys. Union, Nineteenth Annual Meeting*, pp. 243-244. 1938.

No. 181. H. R. Seiwell. Use of Non-Conservative Properties of Sea Water to Physical Oceanographical Problems. *Nature*, Vol. 142, p. 164. 1938.

No. 182. Norris W. Rakestraw and Victor M. Emmel. The Relation of Dissolved Oxygen to Nitrogen in Some Atlantic Waters. *Sears Found. Jour. Mar. Res.*, Vol. I, No. 3, pp. 207-216. 1938.

No. 183. W. H. Johnson. The Effect of Light on the Vertical Movements of *Acartia clausi* (Giesbrecht). *Biol. Bull.*, Vol. LXXV, No. 1, pp. 106-118. 1938.

No. 184. In preparation.

No. 185. C.-G. Rossby. On the Mutual Adjustment of Pressure and Velocity Distributions in Certain Simple Current Systems, II. *Sears Found. Jour. Mar. Res.*, Vol. I, No. 3, pp. 239-263. 1938.

No. 186. H. R. Seiwell. Über die ganz- und halbtägige Mondkomponente der internen Wellen im westlichen Nordatlantischen Ozean. *Annalen der Hydrographie u. maritimen Meteorologie*, Heft X, pp. 485-487. 1938.

No. 187. In preparation.

No. 188. Cornelia L. Carey. The Occurrence and Distribution of Nitrifying Bacteria in the Sea. *Sears Found. Jour. Mar. Res.*, Vol. I, No. 4, pp. 291-304. 1938.

No. 189. Lois C. Lillick. Preliminary Report of the Phytoplankton of the Gulf of Maine. *The Amer. Midland Nat.*, Vol. 20, No. 3, pp. 624-640. 1938.

No. 190. R. B. Montgomery. Circulation in Upper Layers of Southern North Atlantic Deduced with Use of Isentropic Analysis. *Papers in Physical Oceanography and Meteorology*, Vol. VI, No. 2, pp. 1-55. 1938.

No. 191. Jean P. Todd. Shoal-water Deposits of the Bermuda Banks. *Jour. Sedimentary Petrology*, Vol. 9, No. 1, pp. 8–13. 1939.

No. 192. H. R. Seiwell. Die Verwendung der Verteilung von Sauerstoff auf die physische Ozeanographie des Karibischen Meeresgebietes. *Gerlands Beiträge zur Geophysik*, Bd. 54, Heft 4, pp. 1–7. 1939.

No. 193. George L. Clarke and Harry R. James. Laboratory Analysis of the Selective Absorption of Light by Sea Water. *Jour. Optical Soc. Amer.*, Vol. 29, pp. 43–55. 1939.

No. 194. Henry B. Bigelow and Mary Sears. Studies of the Waters of the Continental Shelf, Cape Cod to Chesapeake Bay. III. A Volumetric Study of the Zooplankton. *Mem. Mus. Comp. Zool.*, Vol. LIV, No. 4, pp. 183–378. 1939.

No. 195. George Wald. On the Distribution of Vitamins A_1 and A_2. *Jour. Gen. Physiol.*, Vol. 22, No. 3, pp. 391–415. 1939.

No. 196. Alfred C. Redfield. The History of a Population of *Limacina retroversa* during its Drift across the Gulf of Maine. *Biol. Bull.*, Vol. LXXVI, No. 1, pp. 26–47. 1939.

No. 197. Sidney C. T. Hsiao. The Reproductive System and Spermatogenesis of *Limacina* (*Spiratella*) *retroversa* (Flem.). *Biol. Bull.*, Vol. LXXVI, No. 1, pp. 7–25. 1939.

No. 198. W. J. Clench and C. G. Aguayo. Notes and Descriptions of New Species of Calliostoma, Gaza and Columbarium (Mollusca); Obtained by the Harvard-Habana Expedition off the Coast of Cuba. *Mem. Soc. Cub. Hist. Nat.*, Vol. 12, No. 5, pp. 375–384. 1938.

No. 199. Fenner A. Chace, Jr. Reports on the Scientific Results of the First *Atlantis* Expedition to the West Indies, under the joint Auspices of the University of Havana and Harvard University. Preliminary Descriptions of One New Genus and Seventeen New Species of Decapod and Stomatopod Crustacea. *Mem. Soc. Cub. Hist. Nat.*, Vol. 13, No. 1, pp. 31–54. 1939.

No. 200. Pedro J. Bermúdez. Resultados de la Primera Expedicion en las Antillas del Ketch *Atlantis* bajo los Auspicios de las Universidades de Harvard y Habana. *Mem. Soc. Cub. Hist. Nat.*, Vol. 12, No. 5, pp. 385–388. 1938.

No. 201. George L. Clarke. The Utilization of Solar Energy by Aquatic Organisms. *Amer. Assoc. Adv. Sci.*, Publ. No. 10, pp. 27–38. 1939.

No. 202. Clinton M. Osborn. The Physiology of Color Change in Flatfishes. *Jour. Exper. Zool.*, Vol. 81, No. 3, pp. 479–515. 1939.

No. 203. Martin D. Burkenroad. Further Observations on Penaeidae of the Northern Gulf of Mexico. *Bull. Bing. Oceanographic Coll.*, Vol. VI, Art. 6, pp. 1–62. 1939.

No. 204. Fred B. Phleger, Jr. Foraminifera of Submarine Cores from the Continental Slope. *Bull. Geol. Soc. Amer.*, Vol. 50, pp. 1395–1422. 1939.

No. 205. Talbot H. Waterman, Rudolf F. Nunnemacher, Fenner A. Chace, Jr., and George L. Clarke. Diurnal Vertical Migrations of Deep-water Plankton. *Biol. Bull.*, Vol. LXXVI, No. 2, pp. 256–279. 1939.

No. 206. Sidney C. T. Hsiao. The Reproduction of *Limacina retroversa* (Flem.). *Biol. Bull.*, Vol. LXXVI, No. 2, pp. 280–303. 1939.

No. 207. W. H. Johnson and J. E. G. Raymont. The Reactions of the Planktonic Copepod, *Centropages typicus*, to Light and Gravity. *Biol. Bull.*, Vol. LXXVII, No. 2, pp. 200–215. 1939.

No. 208. Louis A. Toth. Renal and Vascular Responses to Epinephrine Injections in Glomerular and Aglomerular Fish. *Amer. Jour. Physiol.*, Vol. 126, No. 2, pp. 347–353. 1939.

No. 209. John A. Young, Jr. Minerals from Deep Sea Cores and Surface Deposits of Bermudian Calcareous Sediments. *Amer. Jour. Sci.*, Vol. 237, pp. 798–810. 1939.

No. 210. Henry B. Bigelow and William C. Schroeder. Notes on the Fauna above Mud Bottoms in Deep Water in the Gulf of Maine. *Biol. Bull.*, Vol. LXXVI, No. 3, pp. 305–324. 1939.

No. 211. Talbot Howe Waterman. Studies of Deep-sea Angler-fishes (Ceratioidea). I. An historical survey of our present state of knowledge. II. Three new species. *Bull. Mus. Comp. Zool.*, Vol. LXXXV, No. 3, pp. 65–94. 1939.

No. 212. George L. Clarke. The Relation between Diatoms and Copepods as a Factor in the Productivity of the Sea. *Quart. Rev. Biol.*, Vol. 14, No. 1, pp. 60–64. 1939.

No. 213. A. A. Abramowitz. The Pituitary Control of Chromatophores in the Dogfish. *Amer. Nat.*, Vol. LXXIII, pp. 208–218. 1939.

No. 214. George L. Clarke and David D. Bonnet. The Influence of Temperature on the Survival, Growth and Respiration of *Calanus finmarchicus*. *Biol. Bull.*, Vol. LXXVI, No. 3, pp. 371–383. 1939.

No. 215. In preparation.

No. 216. Bostwick H. Ketchum. The Absorption of Phosphate and Nitrate by Illuminated Cultures of *Nitzschia Closterium*. *Amer. Jour. Bot.*, Vol. 26, No. 6, pp. 399–407. 1939.

No. 217. H. R. Seiwell. Some Applications of Statistical Methods to Problems in Modern Physical Oceanography. *Proc. Industrial Statistics Conference*, held at Mass. Inst. Tech. Sept. 8 and 9, 1938. Pitman Publishing Corporation, pp. 156–173. 1939.

No. 218. Pedro J. Bermúdez. Resultados de la Primera Expedicion en las Antillas del Ketch *Atlantis* bajo los Auspicios de las Universidades de Harvard y Habana. Nuevo Género y Especies Nuevas de Foraminiferos. *Mem. Soc. Cub. Hist. Nat.*, Vol. 13, No. 1, pp. 9–12. 1939.

No. 219. Bostwick H. Ketchum. The Development and Restoration of Deficiencies in the Phosphorus and Nitrogen Composition of Unicellular Plants. *Jour. Cell.* and *Comp. Physiol.*, Vol. 13, No. 3, pp. 373–381. 1939.

No. 220. C. O'D. Iselin. The Influence of Vertical and Lateral Turbulence on the Characteristics of the Waters at Mid-depths. *Trans. Am. Geophys. Union*, pp. 414–417. 1939.

No. 221. C. O'D. Iselin. Some Physical Factors which may Influence the Productivity of New England's Coastal Waters. *Sears Found. Jour. Mar. Res.*, Vol. II, No. 1, pp. 74–85. 1939.

No. 222. Theodor von Brand, Norris W. Rakestraw and Charles E. Renn. Further Experiments on the Decomposition and Regeneration of Nitrogenous Organic Matter in Sea Water. *Biol. Bull.*, Vol. LXXVII, No. 2, pp. 285–296. 1939.

No. 223. H. R. Seiwell. *Atlantis* Cruise to the Tropical North Atlantic, January to March, 1939. *Trans. Am. Geophys. Union*, pp. 418–422. 1939.

No. 224. W. J. Clench and C. G. Aguayo. Notes and Descriptions of New Deep-water Mollusca obtained by the Harvard-Havana Expedition off the Coast of Cuba. II. *Mem. Soc. Cub. Hist. Nat.*, Vol. 13, No. 3, pp. 189–197. 1939.

No. 225. Pedro J. Bermúdez. Resultados de la Primera Expedicion en las Antillas del Ketch *Atlantis* bajo los Auspicios de las Universidades de Harvard y Habana. Foraminiferos del Género Recurvoides, descripción de una Especie Nueva. *Mem. Soc. Cub. Hist. Nat.*, Vol. 13, No. 2, pp. 57–61. 1939.

No. 226. H. R. Seiwell. The Effect of short period Variations of Temperature and Salinity on Calculations in Dynamic Oceanography. *Papers in Physical Oceanography and Meteorology*, Vol. VII, No. 3, pp. 1–32. 1939.

No. 227. H. R. Seiwell. Daily Temperature Variations in the Western North Atlantic. *Jour. d. Conseil*, Vol. XIV, No. 3, pp. 357–369. 1939.

No. 228. Norris W. Rakestraw, Clifford E. Herrick, Jr., and Wm. D. Urry. The Helium-Neon Content of Sea Water and its Relation to the Oxygen Content. *Jour. Amer. Chem. Soc.*, Vol. 61, pp. 2806–2807. 1939.

No. 229. Edward M. Brooks. Transport and Convergence of the North Atlantic Drift Current Computed from the Average January Pressure Distribution. *Sears Found. Jour. Mar. Res.*, Vol. II, No. 2, pp. 163–167. 1939.

No. 230. Floyd M. Soule. Consideration of the Depth of the Motionless Surface near the Grand Banks of Newfoundland. *Sears Found. Jour. Mar. Res.*, Vol. II, No. 3, pp. 169–180. 1939.

No. 231. In preparation.

No. 232. Gordon A. Riley. Plankton Studies. II. The Western North Atlantic, May-June, 1939. *Sears Found. Jour. Mar. Res.*, Vol. II, No. 2, pp. 145–162. 1939.

No. 233. J. T. Nichols. Young Caranx in the Western North Atlantic. *Bull. Bingham Oceanographic Coll.*, Vol. VII. Art. 2, pp. 1–9. 1939.

No. 234. Albert Eide Parr. Quantitative Observations on the Pelagic Sargassum Vegetation of the Western North Atlantic. *Bull. Bingham Oceanographic Coll.*, Vol. VI, Art. 7, pp. 1–94. 1939.

No. 235. R. B. Montgomery. Observations of Vertical Humidity Distribution above the Ocean Surface and their Relation to Evaporation. *Papers in Physical Oceanography and Meteorology*, Vol. VII, No. 4, pp. 1–30. 1940.

No. 236. George L. Clarke. Variation in the Transparency of Three Areas of the Atlantic throughout the Year. *Ecology*, Vol. 20, No. 4, pp. 529–543. 1939.

No. 237. In preparation.

No. 238. D. Q. Anderson. Distribution of Organic Matter in Marine Sediments and its Availability to Further Decomposition. *Sears Found. Jour. Mar. Res.*, Vol. II, No. 3, pp. 225–235. 1939.

No. 239. In preparation.

No. 240. In preparation.

No. 241. In preparation.

No. 242. In preparation.

No. 243. Pedro J. Bermúdez. Resultados de la Primera Expedicion en las Antillas del Ketch *Atlantis* bajo los Auspicios de las Universidades de Harvard y Habana. Nueva Género y Especies Nuevas de Foraminiferos. *Mem. Soc. Cub. Hist. Nat.*, Vol. 13, No. 4, pp. 247–251. 1939.